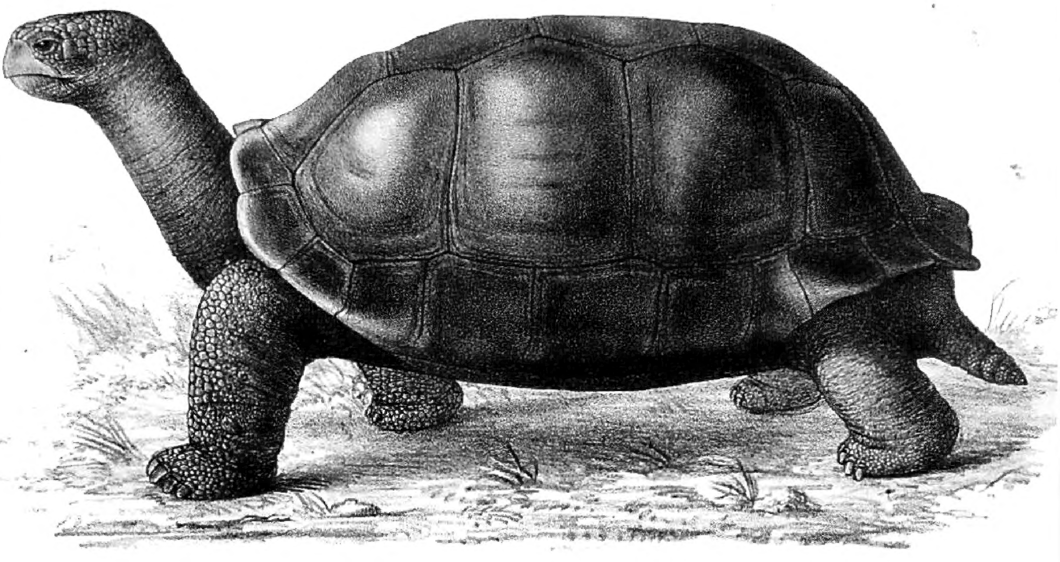
PROCEEDINGS

OF THE

CALIFORNIA ACADEMY OF SCIENCES

(Fourth Series)

Darwin and the Galápagos



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Testudo microphyes, ad ♀
(*North Albemarle.*)

SEPTEMBER 15, 2010 ★ VOLUME 61 ★ SUPPLEMENT II

CALIFORNIA ACADEMY OF SCIENCES

Pacific AAAS

COVER IMAGE

Testudo microphyes Günther, 1875
(=*Geochelone nigra* ssp.)

Based on a specimen said to have come from
"North Albemarle" (Isla Isabela), Galápagos Islands

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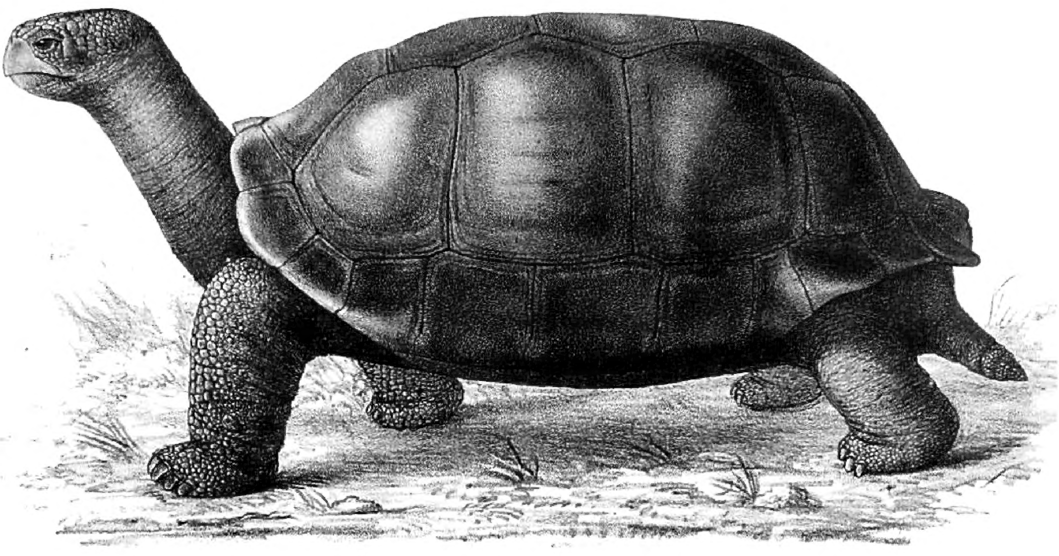
Darwin and the Galápagos

Papers presented at a symposium celebrating the 200th anniversary of the birth of Charles Darwin and the 150th anniversary of the publication of the *Origin of Species* and sponsored by the California Academy of Sciences and the Pacific Division of the American Association for the Advancement of Science
August 14–15, 2009



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Testudo microphyes, ad. ♀
(North Albemarle)

Edited by
Michael T. Ghiselin and Alan E. Leviton

California Academy of Sciences
San Francisco, California, USA

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Acknowledgments

The symposium organizers and editors of this volume wish to acknowledge and express their appreciation to all of those who helped make this event possible. First and foremost, they acknowledge with gratefull thanks Gregory Farrington, Executive Director of the California Academy of Sciences, who generously provided funds to help defray the travel costs of a number of our speakers/authors and who authorized the use of Academy facilities for the two-day program. Also, though too numerous to mention by name, the staff of the Academy who provided the logistical support without which the program would not have succeeded, that is everything from custodial to technical, making sure the microphones, projectors, and, yes, even the mid-session breaks for coffee, all funtioned smoothly. We also want to thank David Mindell, Dean of Science at the Academy, who provided the additional funds we needed to publish this volume.

The Pacific Division of the American Association for the Advancement of Science scheduled its annual meeting in San Francisco so that it could cosponsor the Darwin Symposium. Through the good offices of Roger Christianson, Executive Director of the Division, the Division not only cosponsored the symposium but carried notices about it in its widely-distributed *Newsletter* and published the details of the program and abstracts of all the papers in its *Proceedings* volume for its annual meeting.

Last, but not least, we thank Michele Aldrich and Hallie Brignall for all they did to move this effort along and make this publication a reality in a near record time for a symposium volume.

Michael T. Ghiselin and Alan E. Leviton
California Academy of Sciences
31 August 2010

Darwin and the Galápagos

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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Introduction

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Charles Darwin's visit to the Galápagos Archipelago in 1835 was but a brief episode in a voyage of discovery that opened up a whole new way of thinking about the living world. The Galápagos have become a symbol of scientific accomplishment, a theme for myth and legend, and a laboratory for the study of evolution in action. The two hundredth anniversary of Darwin's birth evoked numerous meetings and celebrations all over the world. It seemed particularly appropriate for the California Academy of Sciences to convene a symposium on Darwin and the Galápagos in the summer of 2009. The Academy has a long history of research in the Galápagos and its collections are the best in the world. When San Francisco was devastated by earthquake and fire in 1906, the boatload of specimens brought back by the schooner *Academy* were the basis for rebuilding the collections. The present volume of essays helps to perpetuate a long tradition of research and publication.

Among the most esteemed participants in that tradition was the late Robert Bowman, to whose memory this volume is dedicated. Alan Leviton and Michele Aldrich, who are experts on the history of the Academy, provide a biographical sketch.

The five-week visit to the Galápagos was part of a five-year voyage around the world. An essay by the paleontologist Jere Lipps helps us to see how the visit fits in with the larger context of the expedition, the main goal of which was to provide hydrographical maps and chronometrical and other measurements for the British navy. Darwin was free to observe and collect anything that might be of scientific interest, but his interest in geology having been aroused while a student at Cambridge University and intensified by reading Charles Lyell's *Principles of Geology*, that subject dominated his research throughout the voyage. Although Darwin was interested in the fauna and flora of the Galápagos, much of his effort there had to do with research on the formation of volcanic islands. These were particularly important because, while still in South America, he had come up with the hypothesis of coral reef formation that made him famous almost immediately upon his return to England.

Edward Larson, who is an historian of science, provides further context in his essay on the Gálapagos before Darwin. When Darwin was a Cambridge undergraduate, preparing for a career as a clergyman, he became acquainted with the writings of natural theologians, notably William Paley, hence *The Natural Theology of Hell*. Early explorers did not consider the archipelago an attractive place or one fitted to human habitation. But by the time Darwin arrived, the Gálapagos had been made habitable by the Ecuadorians. Its scientific interest and natural wonders have turned it into a very attractive place.

Darwin's research in the Galápagos was of great importance to his geological research program. His work there has been under intensive investigation by a team of geologists and historians for several years. We are presented with essays by two members of this team.

Sandra Herbert, a Darwin scholar with special expertise in the history of geology, tells how it

has been possible to provide an explanatory narrative of Darwin's geological investigations in the Galápagos. This kind of historical research is much easier because such a wealth of materials have come down to us. Darwin kept copious notes, and an astonishing amount of material has been preserved and made available to scholars. She compares Darwin's work on geology in the archipelago with his work on geology and botany.

Sally Gibson, who is a geologist, relates Darwin's mineralogical and petrological research in the Galápagos to his predecessors' theories of igneous rock formation. The mineral and whole-rock chemistry of some of his specimens of volcanic rocks have been studied using modern techniques. From his fieldwork Darwin realized that both basalts and trachylites could be formed at the same period of time. He proposed that these two types of volcanic rocks, the crystals of which have differences in specific gravity, may have been formed as a result of the "sinking of crystals" from the same liquid. But this contribution by Darwin in *Volcanic Islands* received only sporadic attention by geologists until after his death.

Jonathan Hodge, a Darwin scholar, asks when and why Darwin first favored the transmutation of species. Hodge answers that no reflections on any Galápagos facts initiated this change of mind. His notes on Galápagos mockingbirds made later in the voyage (in mid-1836) do show, Hodge argues, that Darwin had become a transmutationist, but that this shift was not due to any Galápagos reflections. Hodge conjectures that other facts, not concerning any archipelago, had prompted Darwin's first transmutationist leanings. Later, Hodge emphasizes, Darwin's March 1837 consultations with John Gould radically transformed his thinking, not just about mockingbirds, but about the Galápagos land birds generally and their relationships with mainland American species. Entirely new, general reflections on those relationships then became, Hodge argues, Darwin's main ground for newly-confident, comprehensive transmutationist convictions.

Michael Ghiselin, a philosophical biologist and Darwin scholar, asks a different question, but one that also has to do with how people might interpret the texts. When we, aware of what happened later, read Darwin's pre-*Origin* publications, we easily find passages the evolutionary significance of which became explicit in his later ones. But most of Darwin's contemporaries did not read them that way. It was difficult for him to get the information he needed from his fellow naturalists, and in a few cases he had to explain his evolutionary views to get what he wanted. The case of Alfred Russel Wallace shows how somebody who was thinking along the same lines might make good use of the implicit evidence.

Duncan Porter, an expert on the flora of the Galápagos turned historian, discusses Darwin's credentials and accomplishments as a botanist while on the voyage. The notion that Darwin was ill-prepared to collect plants and study them in the field turns out to be yet another myth. Of course for definitive identification of plant specimens Darwin relied upon the expert judgment of his professional colleagues. We might add that Darwin's later work on plant anatomy and physiology qualifies him as one of the greatest botanists of all time.

Robert Van Syoc, an expert on barnacle systematics, leaves no room for doubt that Darwin was an outstanding systematic zoologist. Darwin's eight years of research on barnacles produced an outstanding monograph — or series of monographs if you prefer. Darwin routinely collected and observed marine invertebrates during the voyage, but unfortunately his Galápagos barnacle specimens were lost. Van Syoc provides ample illustrations of how biologists have built upon the solid foundations that Darwin laid for the study of the group.

John McCosker and Richard Rosenblatt are systematic ichthyologists. They review and update our knowledge of the fish fauna of the Galápagos, which is remarkable for its high level of endemism. As they point out, Darwin collected Galápagos fishes. They were described by his old friend Leonard Jenyns in the *Zoology* of the voyage.

The paleontologist Matthew James discusses the California Academy of Sciences' 1905-06 expedition to the Galápagos. It is a particularly interesting chapter in the history of the Academy for various reasons, not the least of which is that attitudes toward conservation have changed since those days. Also the young men who went on the expedition were there primarily as technicians, not as scientists. These days, the Academy's professional scientists actively participate in field work, as part of their own research. They also focus upon the taxonomic groups upon which they specialize.

John Dumbacher and Barbara West provide a biographical essay on Rollo Beck, who was the leader of the 1905–06 Galápagos expedition. Beck is particularly interesting as an example of a professional collector with little formal education who nonetheless had a considerable impact on ornithology. His accomplishments provide valuable insight into the nature of the collecting enterprise in general.

Peter and Rosemary Grant, evolutionary biologists who have been studying the Galápagos finches for many years, provide us with an overview of their work. They explain how it relates to Darwin's views on species, a topic that interests biologists and historians alike. No doubt Darwin would have been delighted by their documentation of evolution by natural selection as it is going on in natural habitats. As Darwin put it, wonderful forms "have been, and are being, evolved."

The various chapters provide more than just a glimpse of Darwin's life and accomplishment. They represent a good sample of how his investigations progressed, and of the problems with which he was concerned. Inspired by Darwin's example, scientists have returned again and again to the sites and topics that interested him. Darwin's science is evolving, and will continue to do so for the foreseeable future.

A final note — the editors of this volume, want to acknowledge the contributions of Ms Hallie Brignall, former Managing editor of Scientific Publications for the California Academy of Sciences, for her meticulous review of and assistance in preparing the manuscripts for publication.

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

Series 4, Volume 61, Supplement II, No. 2, pp. 5–12, 5 figs. September 15, 2010

Dedication
Robert Irvin Bowman (1925–2006) Remembered

Alan E. Leviton and Michele L. Aldrich
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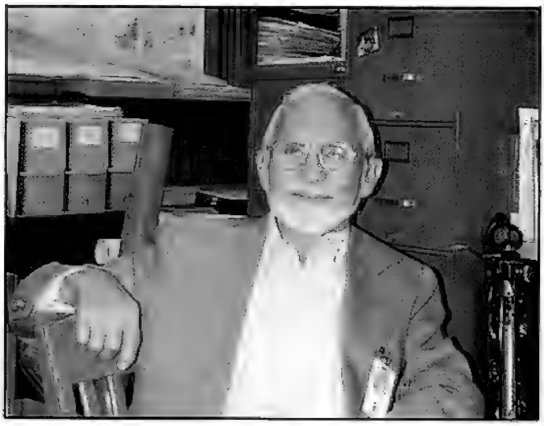
Robert Bowman made his reputation as a teacher at San Francisco State University and as an ornithologist specializing in Darwin's finches. He was educated at Queen's University in Ontario, Canada (B.A., 1948) and at the University of California at Berkeley (Ph.D., 1957). He had a life long interest in the Galápagos Islands and was among the advocates of their preservation. He was active at the California Academy of Sciences and in the Pacific Division AAAS.



Robert Irwin Bowman
(Photo by A.E. Leviton, 6 June 2000)

This is a special moment for us for not only do we celebrate the 200th anniversary of the birth of Charles Darwin but also the 150th anniversary of the publication of the book that challenged the intellectual fiber of the world. However we may argue about how or when Darwin first came to understand the full significance of his experiences in the Galápagos Archipelago, there is no doubt that in time the importance of his observations in the Archipelago was to bear fruit. The Galápagos Islands have ever since played a significant role in furthering our understanding of evolutionary processes and results, and it is assuredly impossible for us to count the number of late 19th and 20th century biologists and, yes, geologists who have been influenced by these enchanted isles. Nonetheless, there emerges from among the crowd one of our own colleagues, one individual — generous, soft-hearted, but no nonsense, highly motivated and energetic Robert Irvin Bowman (Fig. 1), late professor of biology at San Francisco State University who stands out, not by reason of his stature (for he stood barely 5′5″ with shoes on), but by reason of his intellect, drive, and sense of fairness and moderation under trying circumstances. Indeed, with respect to the latter, our colleague Robert Drewes pointed out that during the student unrest in the late 1960s, Bowman served as a campus peacemaker.

Thus today, in addition to celebrating the Darwin legacies, we also commemorate scientific and conservation heritage of Robert Bowman, to whose memory we dedicated the Darwin symposium and now this volume.

Robert Bowman passed away in his 80th year on 12 March 2006. He left so many friends, colleagues, students, and family, we cannot enumerate all. But we do want to take special note here of his wife, Margret, who not only joined us at the symposium session, but who has contributed to science in her own right as a gifted illustrator.

Early in his career, in 1952 as a matter of fact, Bob and Margret visited the Galápagos Islands (Fig. 2), an event that was to lead to his life-long interest in those endemic geospizid birds, more commonly called "Darwin's finches," that inhabit the islands and whose beaks tell an amazing story of evolution and adaptive radiation. In time, Bob also came to see that the biological uniqueness of the islands should be cared for and preserved. He visited the Galápagos many times, 14 in all. As a result, his studies of the finches and of the islands' ecology, and his intensive lobbying for protection of the region, in 1964 not only did the Ecuadorian government set aside more than 1.7 million acres as the Galápagos National Park, but it also awarded Robert the Republic of Ecuador's Medal of Honor for his efforts. Bob's research interests, a commitment to education, including, in the late 1950s, television (Fig. 3), which, for scientific purposes, was still in its infancy, as well as his concern for and commitment to the preservation of the archipelago's unique flora and fauna, led to the establishment of the Darwin Research Station on Isla Santa Cruz, and the Charles Darwin Foundation. Both to this day keep Bob's dedication alive and well.


FIGURE 2. Robert and Margret Bowman on their first trip to the Galápagos Islands in 1952. (Photos courtesy Bowman family).

FIGURE 3. Earl Herald (left) and a youthful 31-year old Robert Bowman (right), October 1956 (*Science in Action* program on the Galápagos Islands). (Photo courtesy Special Collections, Archives, California Academy of Sciences).

In the pages left to us, a few details about Robert are called for. He was born on 19 November 1925 in Saskatoon, Saskatchewan, Canada where he grew up and attended school. In 1948, he graduated from Queen's University in Kingston, Ontario, Canada. He then migrated to California to attend the University of California at Berkeley from where he emerged in 1957 with a Ph.D. and an appointment as Assistant Professor of Biology at San Francisco State University, at the time San Francisco State College, where he already held a teaching appointment, and where he was to spend his entire academic career. His doctoral dissertation on morphological differentiation and adaptation of Galápagos finches, published in 1961), is an extraordinary accomplishment in descriptive and functional anatomy, and the first monograph to be published under the auspices of the Charles Darwin Research Foundation.

As we mentioned a moment ago, Bob accepted a position as Assistant Professor at San Francisco State University where, among other things, he taught, as you might have expected, comparative vertebrate anatomy. Bob was an educator's educator, held in the highest esteem by students and peers alike for his infectious enthusiasm, cheerfulness, and humor, perhaps sometimes on the dry side, but humor nonetheless. Despite a heavy teaching load, Bob never lost interest in the Galápagos or its finches. Peter Grant, in his memoriam notice about Bob (Grant 2007), called attention to Bob's two seminal contributions to the study of Darwin's finches, among which, as we already noted, was his detailed study of the skull anatomy, both descriptive and functional, and related myology, which clearly extended the understanding of adaptive radiation among these birds. The second was his study of how sounds are affected by vegetation and the adaptive significance of song characteristics among the finches that often depended on the habitat in which they lived. These studies were enhanced by another of Bob's unusual talents. David Perlman, *San Francisco Chronicle* Science Editor, observed that Bob had an uncanny ability to mimic the varied chirps and warbles of the birds. David recounted (Perlman 2006) a story passed on to him by one of the members of the 1964 International Galápagos Expedition, a project organized by Robert Usinger, on the faculty of UC Berkeley, and Robert. Here we quote, "the lighthearted and youthful Bowman had set up his recording equipment with its parabolic mirror beneath a stand of trees in an effort to catch the sounds of one of Darwin's thick-beaked ground finches scientifically named *Geospiza fortis* (Fig. 4). 'Come on, birdie, give with the song,' Professor Bowman called and [then] sounded one drawn-out birdlike note. The finch obliged at once with a 'treeeee-you, treeeee-you'" Bob dutifully recorded the call and then, of course, being ever so polite and thoughtful, according to Perlman, he called back to his accommodating songster with a clear "Thanks, fortis!" Inasmuch as Robert expressed his thanks in human language, and in English not Spanish, it is not recorded if the message was properly appreciated!

FIGURE 4. *Geospiza fortis*. (Photo by B. Rosemary Grant, with permission).

Bob readily demonstrated his lightheartedness in other ways as well. Some years ago, as Bob and Alan Leviton were walking down a flight of stairs in John Hensill Hall at San Francisco State University, Leviton asked him what possessed him to grow a full beard. Bob readily explained that because of his smaller stature and youthful appearance he was too often taken for a student, so he

decided to grow the beard to add a bit to his age. And, on another occasion, when informed that among the early mid-19th century members of the fledgling California Academy of Sciences was another Bowman, Amos Bowman, also a Canadian but a geologist, not a zoologist, Robert unhesitatingly grafted him to his family tree, grinning from ear to ear. We could never verify the relationship, though Bob assured us they were connected. Whatever the case, the Academy was the ultimate beneficiary of having both associated with it. Of course, once in awhile, because of his overwhelming curiosity about his surroundings and photography, our dear colleague lost track of time and got himself into a pickle, on this occasion at the Black Diamond Coal Mine on California's Mt. Diablo where, momentarily, he found himself "locked in" behind bars. Mercifully, this was only a momentary incarceration. And, let us not forget those heady days of the feminist movement when gender-neutral vocabulary was being touted and terms such as chairman were no longer acceptable. As a result, committee heads were initially called chairpersons, which then degraded to chair. (As an aside, we recall a thundering outburst by Margaret Mead at a AAAS Council meeting when introduced as the "Chair" of a recently appointed Board committee, "I am not a piece of furniture, I am chairman of the committee!".) Be that as it may, during those days we prepared the *Newsletter* for the AAAS Pacific Division, and, of course, often had to refer to Dr. Bowman, who played so seminal a role in Division activities. To double check both spelling and grammar, we used a checker called "Grammatik®." No getting around it — every time it came to Bowman the program insisted that we substitute the gender-neutral term *Archer*. We spoke to Bob about this, asking if it would not be a good idea if he were to change his name accordingly. Of course, you know what his answer was; we can not repeat what he said here, but you can use your imagination.

FIGURE 5. A thoughtful Robert Bowman, October 1956, addressing questions about his beloved Galápagos finches. (Photo courtesy Archives, California Academy of Sciences).

A penultimate note. Bob became involved with the AAAS Pacific Division in the early 1980s serving first as a member of the Division's Executive Committee, then three times as chair of local organizing committees for subsequent Division annual meetings at San Francisco State University, then as President of the Division, and to the time of his death as Counselor to the Executive Committee. He was indefatigable; if something could not be done, he found a way around the impossible. If some one told him that only the President of the University could authorize something, the next morning Robert was standing at President Corrigan's door; he never came away empty handed. Another of Bob's strengths, especially as a scientist, was his curiosity about the natural world. He was also an avid reader and, for instance, he perused each issue of the weekly *Sci-*

[1] **Note on sources.** As this article was being readied for press, Margret Bowman and her children were in the process of donating Bob's scientific papers and correspondence, field note books, laboratory records, and other materials to the Archives of the California Academy of Sciences for the use of future generations of ornithologists as well as historians of science.

ence magazine, each issue of *Nature*, as well as other journals that crossed his desk, and he thoughtfully digested their contents. He loved Pacific Division's meetings because of their interdisciplinary nature, and he was an endless source of ideas on cutting-edge topics for potential symposia and presentations at them. The Division was enriched by his presence as was the California Academy of Sciences. At the latter institution, he had extensive interactions with its scientific staff and, in addition to being a Fellow, he also served with distinction as a scientist member of its Board of Trustees. In 2001, Bob was the recipient of the Fellows Medal of the California Academy of Sciences, the Academy's highest award given to those scientists who have distinguished themselves in their science and their service to the community.

Bob's dear friends, Rosemary and Peter Grant, recently sent us a note in which they observed, "Bob was an exceptionally lucid communicator, whose verbal skills were complemented by his artistic skills in displaying all kinds of illustrations in his articles, from bones and muscles to sound spectrograms." Not only do we fully concur with Peter and Rosemary, but we must add that Bob's writings and service as editor of books on the Galápagos are also well-know to most of the readers of this volume, notably the two publications for which he served both as editor and contributor, the 1963 International Galápagos Expedition's *The Galápagos* (UC Berkeley, 1966) and *Patterns of Evolution of Galápagos Organisms* (AAAS Pacific Division, 1983), the latter including Bob's seminal paper on the "Evolution of Song in Darwin's Finches", and, were this not enough, we take special note of the role he played in the establishment of the Galápagos National Park, the Charles Darwin Research Station, and the Charles Darwin Foundation, these being just a few of the enduring legacies of our friend, scholar, and teacher. We owe much to Robert Bowman, and it is with affection that we dedicated the symposium and now this publication to honor him and his memory.

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Charles Darwin and H.M.S. *Beagle*: Besides Galápagos

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"The voyage of the *Beagle* has been by far the most important event in my life and has determined my whole career." Charles Darwin (*in* F. Darwin, 1887:61)

Although Charles Darwin and the Galápagos Islands are forever intertwined, it was not that way on H.M.S. *Beagle*. Darwin arrived in the Galápagos on September 16, 1835, after spending 1364 days of a total of 1737 on the voyage of the *Beagle*, chiefly exploring parts of east and west South America, especially in the south. The ship's crew and Captain Robert FitzRoy were already long overdue on the planned 2-year voyage when they arrived at Galápagos, and they were getting anxious for home. Once the *Beagle* left South America, the pace of voyaging increased so that only a few days would be used at stops on its way home. Thus, the Galápagos were short-changed compared with other places — Brazil, the Pampas, Falkland Islands, Tierra del Fuego, Isla Chiloé, mainland Chile, even little St. Jago in the Cape Verde Islands. The *Beagle* spent 31 days cruising among the Galápagos Islands, at one period blown off course. Darwin, who had great expectations of viewing the volcanic geology of the islands, spent only 19 days or parts of days ashore on only four of the 15 major islands. These days were chiefly devoted to geologic endeavors. While in the Galápagos, he did observe and collect the unique fauna and flora but had no significant insights into them until well after his return to England, when they were examined mainly by other experts and after he had studied his notes. The growth of Darwin on the *Beagle* was chiefly in geology; biology came later. Not that he ignored the biology, he did not. He observed and collected many animals and plants, and he had thoughts about the distribution of animals, but he did not develop broader theories and ideas as he did in geology.

Darwin's development before, during and after the voyage has been recounted in many books and articles. His voyage too has been well documented, perhaps no better than in his own words published in his *Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of H.M.S.* Beagle *Round the World*, first published in 1839 and later in 1845 (2nd edition), and still later as the *Voyage of the Beagle*. These accounts incorporate information from his diary, notes, and later thoughts and research, and they also rearrange some of the timing. Nevertheless, it is the leading source of information on Darwin's voyage on *Beagle* and it is very good reading. The huge amount of material about the voyage from many sources cannot be easily told in a single short paper, but that is not the object of this essay. Instead, I intend to summarize Darwin's work besides that he did on the Galápagos in order to set his short time there into the context of the larger voyage. Rather than cite and repeatedly cite the many sources of information, I provide a list of references at the end that were particularly useful to me.

United Kingdom, 1809–1831: The Making of a Naturalist

FIGURE 1. Charles Darwin's birthplace, The Mount, Shrewsbury, England. A. The Mount House as it is today. It is a private local government building now, but visitors are allowed at times. Darwin was born on the second floor, said to be the room with the window above and to the left of the entrance portico. B. The River Severn in 2010 and trees and brush (right) at the bottom of The Mount property. Darwin fished and collected in these places 200 years ago. (Photos by Jere H. Lipps, 2010.)

Charles Darwin was born at his well-to-do family's home known as The Mount House (Fig. 1A) in Shrewsbury, Shropshire, England, on Sunday, February 12, 1809. The Mount, a hill just north of the center of Shrewsbury and across the River Severn, was chosen as the Darwin family home site by Doctor Robert Darwin, Charles's father, and The Mount House was finished just nine years before Charles appeared. Charles Darwin, although he did not know it, began his training as a naturalist for the *Beagle* almost as soon as he could walk. The Mount, in the early 1800s, was surrounded by trees and low vegetation, and the River Severn ran at its base (Fig. 1B). The young Charles was intrigued with most everything he saw in this semi-wilderness as well as in the family's garden. He collected many different organisms but his favorite, like many naturalists before and since, was beetles. He had a collector's passion, he wrote, and he did not limit himself to animals and plants but included stamps, coins and minerals as well. In his egg collecting, Darwin was particular to take only one from each nest in order to let the others live — he had an early sense of conservation as well. Charles Darwin, as was common among the well-to-do families, learned to shoot at a young age. He was particularly adept at shooting birds and considered himself a good shot. He especially enjoyed shooting outings with his uncle Josiah Wedgwood II at Maer Hall in Staffordshire. These traits and habits would serve him well on the *Beagle*.

Charles was sent by his father to Shrewsbury School for a basic classical education, but the young man found it boring and stifling. He did not like it and did not do particularly well. Robert Darwin thought his son was not a good student and finally removed him from the school at age 16 and sent him to the University of Edinburgh to study medicine. Although Charles attended patients for a summer, he did not find that or the dissections in class at all interesting or tolerable. At Edinburgh, he became associated with science, scientists and scientific societies, interacting with all of these in serious ways. Nevertheless, he quit his medical training. His father then decided to send him to Cambridge University to study theology. There Darwin enhanced his interest in natural history, and relished the interactions with the professors, particularly John Stevens Henslow in botany and natural history and Adam Sedgwick in geology.

Charles Darwin had the good fortune to do geological field work during the summer of 1831 with Sedgwick. Starting on August 5, Sedgwick and Darwin left Shrewsbury together for a geological tour including map making in Wales. After just seven days, Darwin and Sedgwick separated

and Darwin continued on in Wales arriving back in Shrewsbury on August 29. There he found a letter from Henslow inquiring about his interest in a position as a naturalist on a voyage around the world, and another letter with a formal invitation to join H.M.S. *Beagle* as a naturalist and companion to Captain Robert FitzRoy.

H.M.S. *Beagle*, 1828–1831: Background to a Famous Voyage

Beagle is a name that has been used for eight ships of the British Royal Navy in service between 1800 and 2007. It also was used for a Martian lander (*Beagle 2*) operated by the European Space Agency that crashed on Mars in December 2003 and for several boats of the Charles Darwin Research Station on the Galápagos Islands. The name, taken from the dog breed, was well used by the British. The most famous *Beagle*, however, was the second H.M.S. *Beagle,* on which Darwin later sailed. This *Beagle* was built as a 10-gun brig at the Woolwich Dockyard on the Thames River and was finished in 1820. Lying unused for much of the next five years, she was re-rigged as a barque for surveying duties.

Commanded by Captain Pringle Stokes, the second H.M.S. *Beagle* commenced its first voyage, setting sail in 1828, as a hydrographic ship mapping in the waters of southern South America, particularly in Tierra del Fuego, Strait of Magellan, and Patagonia. This *Beagle* sailed as a companion ship to the larger H.M.S. *Adventure* during much of this work. Stokes, said to be somewhat unstable and depressed, shot himself on August 2, 1828; he died ten days later in the Strait of Magellan, leaving the ship without a captain. Lieutenant W.G. Skyring, Executive Officer of the *Beagle*, was appointed to command the ship, taking her to Rio de Janeiro where young Robert FitzRoy (aged 23) was made temporary captain on December 15, 1828. FitzRoy decided to continue the hydrographic surveying of Tierra del Fuego originally assigned to the voyage. While in Tierra del Fuego, a long boat belonging to *Beagle* had been sent to examine more remote parts of the area but some local native Fuegians took it, leaving its crew stranded. After searching widely in coves and along the coast of southern Tierra del Fuego for the missing boat, FitzRoy found the crew and learned of the Fuegian theft. He then decided to hold several Fuegian natives hostage on board *Beagle* for exchange of the stolen boat. This did not work, so all but four of the natives were released. FitzRoy decided that these four natives, named by the ship's crew Fuegia Basket (a girl, aged 9), York Minister (male, 26), James "Jemmy" Button (male, 14), and Boat Memory (male, 20), would be taken back to England at his own expense. FitzRoy felt complete responsibility for the Fuegians, and he took care to protect them as best he could on the ship and later in England. The Captain was also troubled by anomalous and confusing magnetic measurements made in Tierra del Fuego that he attributed to the possible presence of magnetic minerals in the mountains nearby, and thought he needed a geologist to help solve the problem. FitzRoy continued working with the *Beagle* in South America finally returning to England in October 1830. One of the Fuegians, Boat Memory, died, apparently of smallpox, in Plymouth in November 1830, and FitzRoy became deeply concerned for the fate of the other three natives. This and his desire to return to South America to finish the hydrographic work led him to speak for another voyage to complete these aims.

The Second Voyage of H.M.S. *Beagle*, 1831–1836: Charles Darwin Becomes Unofficial Naturalist of the Ship

The events on the first voyage of the second *Beagle* were critical in framing the second and most famous voyage of that *Beagle.* FitzRoy had high hopes of continuing the hydrographic surveying he had already done. He was determined to return the Fuegians to Tierra del Fuego and he

wanted to take a geologist to Tierra del Fuego in order to investigate the anomalous magnetism he had puzzled over earlier. Upon his return to England, however, he discovered to his great disappointment, that the Lords of the Admiralty were no longer interested in supporting another voyage to South America. After some persuading by others, Captain Beaufort in particular, and requests by FitzRoy, the Admiralty agreed to allow the return of the Fuegians, and at the same time also required further surveys of South America and acquisition of navigational, magnetic and astronomical measurements at meridians around the world, according to their voluminous instructions. FitzRoy agreed to this and was appointed captain of H.M.S. *Beagle* (actually the second choice for a ship), which was re-commissioned on 4 July 1831. He began planning for a two to perhaps three-year circumnavigation of the globe.

FitzRoy also proposed to Captain Beaufort of the Admiralty to begin a search for a naturalist who could be his companion to accompany him on the voyage. Beaufort wrote to Professor Peacock of Cambridge to inquire about finding a suitable person. Peacock, who commonly arranged for naturalists to accompany ships, contacted Professor Henslow. Henslow, who was much impressed by Charles Darwin's capabilities in natural history, then wrote to Darwin, who received the letter and invitation upon his return from his field trip to Wales with Sedgwick. Darwin was excited but his father, Dr. Robert Darwin, thought the idea was inadvisable, telling Charles that if he could find a thoughtful man who believed it was a wise adventure, he could go. Charles did find exactly the right person—his uncle Josiah Wedgwood II, an influential family member well respected by the elder Darwin. Wedgwood along with Charles went to The Mount to persuade Robert to support Charles's desire to join the *Beagle* voyage as naturalist. The father was convinced and could no longer resist Charles's request. Charles Darwin, after an interview with Robert FitzRoy in London, was deemed a good prospect for the position, and FitzRoy invited him to be his guest for the duration of the voyage, acting in the unpaid role of naturalist. As was usual on ships of the time, the official naturalist was the ship's surgeon Robert MacCormick, who later in 1832 at Rio de Janiero would leave the ship because of bad feelings between himself and the Captain. Indeed, MacCormick was angry with FitzRoy for ignoring him and favoring Darwin, and he thought Darwin had usurped his official naturalist duties when he observed Darwin's collecting activities at previous stops of the ship. Although Darwin and the surgeon had few interactions, Darwin did not think too highly of him anyway; indeed, he wrote his sister Caroline "He is no loss" (Burkhardt 2008:115). Darwin was to pay his share of the expenses of his shared accommodations with FitzRoy and all of the costs of his equipment and supplies. FitzRoy did allow the ship's crew to help Darwin in his work and to ship his specimens back to Henslow in England.

At this time Darwin thought of himself more as a geologist than a biologist. Indeed, although he often called himself a "naturalist", the only time he ever referred to himself as something else, he chose "geologist". Later, he even proposed himself to be Secretary of the Geological Society, London, a position he did obtain after the voyage. Thus Darwin was invited aboard *Beagle* by FitzRoy as an intellectual companion as well as unofficial naturalist and one who might assist him with his magnetic problems in Tierra del Fuego. FitzRoy received the approval of the Lords of the Admiralty to include Darwin on the voyage. Unusual by today's standards, the crew of the *Beagle* was young. Captain FitzRoy was 26 and Darwin was only 22 when the ship left England.

The mission and needs of the *Beagle's* voyage would dictate where Darwin would go and what he would see. Darwin was especially well prepared to carry out the duties of naturalist by his early experiences of collecting all sorts of natural objects, his skill at shooting birds and small animals, and his developing knowledge and interest in geology. The *Beagle* carried a good library of natural history and geology books that Darwin perused. And, although Darwin had read Humboldt before the voyage and was given a copy of the first volume of Lyell's *Principles of Geology* by

FitzRoy at the start of the voyage, his brother, Erasmus, would gladly send Charles books that he requested during the voyage. He was also broadly interested in other scientific fields, especially anthropology ranging from the more primitive peoples to the European immigrants in the countries he visited. All of this, and an open mind, an ability to record his observations and collections, and especially to draw reasonable but not always correct conclusions, made Darwin an excellent naturalist, even if it was an unofficial position on the ship. Darwin did not start the voyage with predetermined ideas regarding biology or geology, but he learned as he went. While he may have had glimmers of evolution on the voyage, for example, he did not fully develop those and most other ideas until he was back in England where he had time to absorb and study his notes and specimens, and to consult with other scientists.

The Atlantic Islands, December, 1831–March, 1832

Darwin, like many people, was fascinated by islands, and he even had plans to visit the Canary Islands before he was offered the position on *Beagle.* Islands attracted Darwin because they are isolated, often contain different or unusual biotas, are generally simple in ecological structure, and can be neatly circumscribed and thus appear to be more readily understood than the contiguous geology and biology of much larger continents. So Darwin looked forward to the voyage with great anticipation.

Beagle left England from Devonport (Fig. 2 [1]) with the Canary Islands as the first stop (Fig. 2 [2]) on December 21, 1831, after two earlier attempts to depart that failed due to high seas. As soon as the *Beagle* cleared the coast and was in the open water of the Bay of Biscay, she began to roll with the swells as she was driven before the wind. FitzRoy himself found the crossing of the

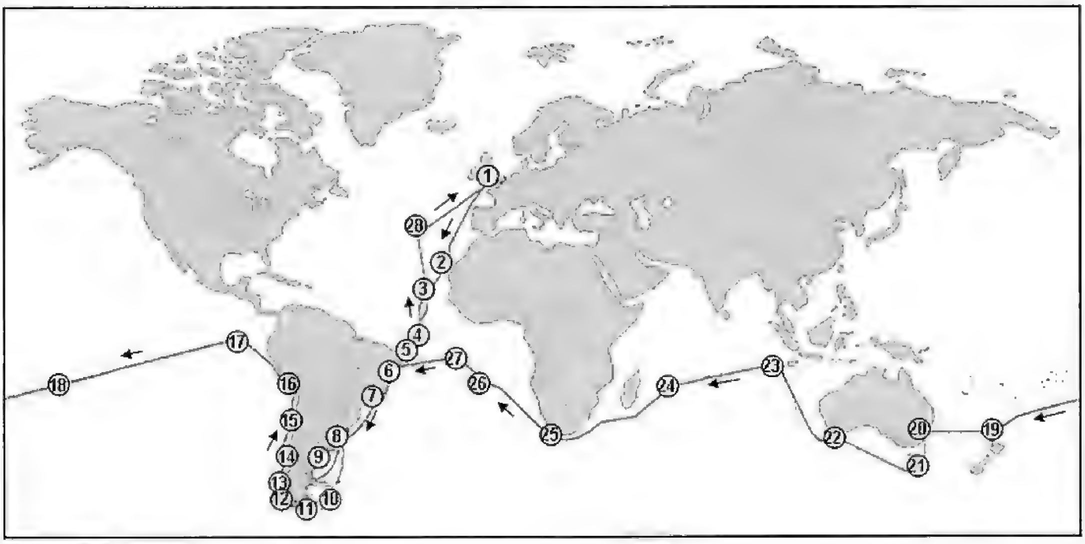

FIGURE 2. Route of the H.M.S. *Beagle,* 27 December 1831 to 2 October 1836, showing the major stops where Charles Darwin conducted field work. The *Beagle* and Darwin visited three continents (South America, Australia and Africa) and over 40 islands besides Galápagos. The places Darwin visited, in the order of visit, were: 1. left Devonport, England; 2. Canary Islands; 3. Cape Verde Islands; 4. St. Paul's Rocks; 5. Fernando Noronha Island; 6. Bahia, Brazil; 7. Rio de Janeiro; 8. Maldonaldo and Montevideo, Uruguay, and Buenos Aires, Argentina; 9. El Carmen and the Rio Negro, Argentina; 10. Falkland Islands; 11. Tierra del Fuego, Straits of Magellan and Beagle Channel; 12. Chonos Archipelago, Chile; 13. Isla Chiloé, Chile; 14. Valdivia, Chile; 15. Valpariso, Chile; 16. Callao, Peru; 17. Galápagos Islands; 18. Tahiti; 19. Bay of Islands, New Zealand; 20. Australia (Sydney); 21. Tasmania (Hobart); 22. Western Australia (King George's Sound); 23. Cocos (Keeling) Atoll; 24. Mauritius; 25. Cape Town, South Africa; 26. St. Helena; 27. Ascension Island; 6. Bahia, Brazil (again); 3. Cape Verde Islands (again); 28. Azores; and 1. arrived Falmouth, England. (Map prepared by Jere H. Lipps.)

bay to be "almost as disagreeable" (Stanbury 1977:41) as if the ship had been in a gale. Darwin, on his first day out, got seasick and spent most of his time in his hammock. Indeed, he found that lying horizontally was the only way to find relief from the nausea and sickness that he felt. Such sickness plagued Darwin throughout the entire five-year voyage, prompting him to spend long times off the ship in many ports or in making traverses from one port to meet *Beagle* at another. This, of course, provided Darwin with excellent opportunities to perform his naturalist observations.

Captain FitzRoy intended to put in at various islands to make the detailed measurements required by the Admiralty. Thus, he headed towards the islands dotting the Atlantic Ocean from the Canaries to the Falklands. The misery of the Bay of Biscay continued for 10 days, during which time *Beagle* passed Madeira and Piton Rock at a distance and searched in vain for the rocks known as the Eight Stones. Darwin was excited to approach Tenerife in the Canary Islands (Fig. 2 [2]), perhaps in part for the relief he anticipated from his sickness. But more importantly, he had read Humboldt's description of the island and its biota, and he had even discussed the possibility of a trip there after his graduation from Cambridge. He thus was excited to see Humboldt's island for himself. As soon as *Beagle* dropped anchor, a small boat appeared with health officials from Tenerife. They had heard of a cholera outbreak in England and refused to allow anyone from the ship to land unless they submitted to a 12-day quarantine. Rather than lie at anchor for that time without opportunity to do his work, FitzRoy set sail immediately for the Cape Verde Islands. Disappointed, Darwin could clearly see the brightly colored houses of Santa Cruz as *Beagle* sailed to within a half mile of the island — his dream and plans for walking in the footsteps of Humboldt were gone forever. Passing through the Canary Islands close to Gran Canaria, Darwin could also see the volcanic nature of the islands, and more than a century and a half later, the islands were finally but controversially determined to be the result of tectonic hot spot volcanism.

Continuing south along the African coast, Darwin was disappointed by the Cape Verde Islands (Fig 2 [3]), about 450 km (300 miles) west of Africa, and especially St. Jago (now Santiago) Island, because they were so desolate and miserable due to the exposed lava flows, hot temperatures, and sterile soil, made so by humans cutting the vegetation in past years. As he would at future stops, Darwin recognized and did not approve of the activities of humans that destroyed the landscape and natural beauty. Darwin and his companions made trips into the interior of St. Jago where he found valleys that he thought were formed by marine processes. The tropical plants living in the valleys impressed him and he devoted much space in his notes to the people living there. His interest in people and his observations on them began early in the voyage as well. Now, these islands are also considered to have formed as hot spot volcanoes. On St. Jago and its tiny neighbor Quail Island, he had a close look at these volcanic rocks and he compared them to those at home. Of course, the comparison was of the rock types, not the processes of formation as those differ and the plate tectonic explanations for the islands were far in the future. Likewise, he compared the larger corals living there with the small solitary species he had observed near Edinburgh. Again the differences are great, but his method made him consider the importance of corals. He found in the sea cliffs layers of lava overlying sedimentary rocks containing corals and he noted that they were the same species as those living in the sea nearby. He carefully described the stratigraphy and fossil occurrences at various levels in the outcrops on Quail Island. Darwin was also applying and enhancing his method of both geological and biological comparisons that he would use throughout the voyage. He noted the various sea levels he could recognize on the islands, concluding that the island has both risen and fallen, although he did not know of sea level changes due to ice accumulation and disintegration during the Pleistocene. He recalled his geological instruction from his time in the field with Sedgwick and he applied Lyell's uniformitarian approach, so that he began

to understand the geology of these islands. On St. Jago and Quail Islands he felt he had really worked out and understood the geology. His time on St. Jago was significant because here he began to put the geology and biology into an understandable context, all from his own observations. His use of the comparative method, his detailed observations, and the nature of the landscapes allowed him to draw his own conclusions. St. Jago was an inspiration in how to do field work on his own; the experience served him well throughout the rest of the voyage as he often compared what he learned at St. Jago to new situations at other places. Here Darwin first conceived of a book he might write on volcanic islands. He was not always right, but he was able to understand the broader implications of his observations. His 27 days on St. Jago and Quail Islands were more influential to him than his 17 full days on four of the Galápagos Islands.

After the Cape Verde group, FitzRoy took *Beagle* towards the middle of the Atlantic Ocean and, by means of superb navigation for a single week, arrived at tiny St. Paul's Rocks, nearly at the equator (Fig. 2 [4]) and 870 km (540 miles) from South America. After launching two boats with crews to land, *Beagle* sailed around the rocks taking deep soundings close to them that were correctly thought to indicate they were the top of a submerged mountain. St. Paul's Rocks are neither large nor high, but they were inhabited by a huge number of birds, just as they are today, identified by Darwin as boobies and noddies. On February 16, part of the crew, including Darwin and FitzRoy, went ashore for a few hours, during which time they enjoyed themselves chiefly by killing birds and collecting eggs for food. FitzRoy described how his crew threw stones at the birds and that Darwin successfully used his geological pick in a similar fashion, although he declined to let another crewman use it for fear of breaking the handle. Exactly how many birds were killed by geologic pick remains unknown but the group managed to gather quite a number of them for the ship's tables. Later Darwin used his pick appropriately to collect samples of green and black rock types representing pieces of an intrusion from deep in the earth's mantle on the Mid-Atlantic Ridge upon which St. Paul's Rocks lie. Darwin's description of the rock types was accurate although he did not know their origin then. He also was impressed by the simplicity of the biota — the two birds plus associated insects as well as marine animals. While FitzRoy and Darwin were ashore, another part of the crew fished around the rocks with great success, struggling with sharks. Replenished with abundant birds, eggs and fish, the *Beagle* left St. Paul's Rocks.

The ship continued southwesterly, crossing the equator, where Darwin and others who had never done that before, were treated to an appearance of Neptune and a lot of sloshing water and great fun. On the 19th of February, a small island in Fernando de Noronha Archipelago (Fig. 2 [5]), about 354 km (220 miles) off the Brazilian coast, was sighted. The group belonged to Brazil as it does now. The following day, FitzRoy went ashore on the main island, marked by a spectacular, steep and barren volcanic peak, to make measurements with his instruments. These islands were all volcanic as well, and forested. They contained an array of insects, all noted by Darwin in just a few hours. The ship left in the evening of same day without taking on water.

South America

Now began nearly two years' work along the coast of eastern South America in Brazil, Uruguay and Argentina, including port calls at Bahia (Salvador), Rio de Janeiro, Maldonaldo, Montevideo, Buenos Aires, and Bahia Blanca. After 10 months, FitzRoy interrupted his survey of Brazil, Uruguay and Argentina to head south in the Austral summer for nearly three months in Tierra del Fuego to deliver the three Fuegians to their homeland, to set up a mission in their territory, and to show the flag at the Falkland Islands, recently acquired from Argentina. Finishing for the time-being in the Falklands in April 1833, *Beagle* then headed back north to finish surveying in

Uruguay and Argentina. Importantly for Darwin, plenty of opportunity would be available for long excursions overland while in each of those countries and to spend time in the relatively unexplored islands at the tip of South America. During this time, Darwin chiefly made observations and collections on the biology and paleontology he encountered although he was always ready to do geology. Much of the geology was covered by vegetation or was very similar over long stretches of coastline. The vegetation in the tropical regions of Brazil always amazed him and he was thrilled to find giant mammalian fossils at several places on his excursions. Once FitzRoy was done on the east coast on 22 January 1834, he turned back to finish work at Tierra del Fuego and the Falkland Islands, finally entering the Pacific Ocean through the Strait of Magellan and the Cockburn Channel on 11 June 1834.

Eastern South America, February-December, 1832 and April, 1833–January, 1834

Arriving at Bahia on mainland Brazil (Fig.2 [6]) on 28 February 1832, *Beagle* stopped for two weeks. Darwin left the ship for treks into the countryside from the town, observing the luxurious vegetation and abundant insects, and collecting samples of all. This, his first encounter with the continent's tropic botany, impressed him enormously. Of Bahia and its vegetation he wrote his sister Caroline: "The scenery here chiefly owes its charm to the individual forms . . ." (Burkhardt 2008:108). The people and how they lived also interested him. He was fascinated by their lodgings, dress and trades. Darwin, an abolitionist, also was appalled at the slavery he encountered first at Bahia. FitzRoy too believed that slavery was "an evil long foreseen and now severely felt" (Stansbury 1977:56) but also thought that the Brazilians treated their slaves well for the most part. At dinner one night, the Captain recounted his recent visit to a plantation where the owner presented slaves who all replied "no" when asked if they'd rather be free. Darwin sharply replied that the answer is what one would expect of slaves standing in front of their master and, further, he asked FitzRoy if he actually believed that answer. FitzRoy took offense at Darwin's boldness — perhaps as much about how Darwin addressed him as Captain as about the issue — resulting in an order that Darwin could no longer take meals at the Captain's table. Darwin had been thrown out of the shared accommodations with FitzRoy and figured that his voyage was over. But this display of anger, as it turned out, was something FitzRoy engaged in commonly with others. In a just few hours FitzRoy's anger subsided and he sent Darwin a message inviting him back to the table, and the voyage continued as before.

Beagle then left for the Abrolhos Islands, just 32 km off the coast (Fig. 2 [6]), to complete lead-line bathymetric surveys in the difficult shallow waters near them. On the islands Darwin was impressed by the vivid green vegetation comprised of just a few species, the abundant spiders and rats and, as he put it, a "saurian" under every rock. In the sea, he found that these volcanic islands were surrounded by corals growing in the adjacent shallow waters, reminding him of the corals seen around the Cape Verde Islands. He began to think about ideas on the relationship of volcanic islands to coral reefs; he would develop this idea more fully three and a half years later in the Pacific. Darwin was trying to articulate the processes that accounted for the objects and organisms he observed and collected, especially those in geology.

After arriving at Rio de Janeiro (Fig. 2 [7]) on April 3 and receiving the first mail from home, FitzRoy began a style of surveying that took considerable time to map the various coastlines. As the ship moved slowly and repetitively along the coast and offshore islands, Darwin had time to leave the ship and explore inland for long periods, sometimes being picked up again by the ship where he left it or meeting it at another place far away. Again at Rio de Janiero (Fig. 3), Darwin left the ship as it returned north to survey near Bahia and remained ashore from April 6 to July 5.

In April, Darwin and several others, including a local Englishman, went northeast for about 100 miles to Rio Macae where they spent three days at an estate. Darwin took special note of the biota, again writing to Caroline "Forest, flowers & birds, I saw in great perfection, & the pleasure of beholding them is infinite." (Burkhardt 2008:116.) He collected many insects and spiders, observed planarians, and again encountered slavery, which repelled him. Returning the night of the 23d of April, he arranged for a small house near Botafogo Bay across from Sugarloaf (Fig. 3) and below the Corcovado in Rio. He and two shipmates lived there, visiting Rio proper and packing natural history specimens for shipment to England. When *Beagle* returned from its work at Bahia, the three men were shocked to learn that three other members of the crew had died of disease. They moved back on board *Beagle* on June 28, and the ship left Rio for Montevideo, Uruguay, on July 5. The passage to Montevideo took 21 days during which Darwin made observations of pelagic animals collected in his nets. For a few days of the trip just before arriving at Montevideo, rain and lightning occurred around the ship. Both Darwin and FitzRoy were impressed and wrote about the electrical displays: ". . . the darkness of the sky is interrupted by the most vivid lightning. The tops of our masts and higher yard ends shone with the electric fluid playing about them" (Stansbury 1977:73), wrote Charles Darwin about this, St. Elmo's Fire.

FIGURE 3. Modern Rio de Janeiro. In 1833, it was a small tropical town surrounding a beautiful harbor. Upon arrival there, Darwin wrote to Caroline: ". . . it is at present rather too novel to behold Mountains as rugged as those of Wales, clothed in an evergreen vegetation & the tops ornamented by the light form of the Palm.—The city, gaudy with its towers & Cathedrals is situated at the base of these hills, & command a vast bay, studded with men of war the flags of which bespeak every nation." (Burkhardt 2008:109.) Although he would be surprised at the number of people living there now (close to 7 million), and to see the extent of the city and its tall buildings, Darwin would probably still describe Rio in much the same language. He and two shipmates lived in a small house across Botafogo Bay from Sugarloaf, the bald mountain shown here on the right of the bay. (Photo by Jere H. Lipps, 1983.)

Arriving at Montevideo on July 26, the ship was ordered by the British Frigate *Druid* to prepare for hostile action because of an uprising in Montevideo that impinged on a British citizen. Darwin was not particularly impressed writing that "The revolutions . . . are quite laughable; some few years ago in Buenos Aires, they had fourteen revolutions in twelve months; things go as quietly as possible. . . ." (Stansbury 1977:72.) Thus the crew, with Darwin helping, went ashore to stem the revolution, which ended quietly. A few days later on anchoring at Buenos Aires, *Beagle* again encountered problems — an Argentine vessel fired two shots (one blank) at *Beagle* ordering her not to anchor. FitzRoy, outraged, exchanged words with the Argentine captain and returned quickly to Montevideo. Later, *Druid* went to Buenos Aires and extracted an apology. Having avoided entanglement in local problems, *Beagle* started slowly surveying south from Rio de la Plata to Bahía Blanca. Before leaving Montevideo, Darwin was able to ship his first lot of specimens, packed in Rio de Janiero, to England and Prof. Henslow.

In the area of Bahía Blanca, Darwin made discoveries and observations that encouraged him to continue longer term explorations than the few weeks available on this cruise. Near Bahia Blanca from early September to mid-October, 1832, Darwin found the fossil remains of a number of

large Pleistocene mammals at Punta Alta, began to understand the geology in the region, and encountered the modern fauna of the Pampas. This work was terminated on October 30 by FitzRoy's plans to return to Buenos Aires and Montevideo and then to proceed to Tierra del Fuego during the Austral summer to return the Fuegians to their homeland. Darwin was not done with the Pampas and southern Argentina, as the ship would return to the region of Bahia Blanca. Then he would spend most of August and September, 1833, exploring the Pampas with overland treks from Rio Negro to Bahía Blanca and then on to Buenos Aires.

During these times on the coast and Pampas of Argentina, Darwin, although he continued his natural history collecting, was particularly engaged in four interests: 1. the fossil record of the region; 2. the geology of the coastal plain; 3. the existing animals of the region; and 4. the gauchos, Indians and Spanish life styles and interactions.

Among the fossils were a host of larger mammals virtually unknown previously. In coastal and river exposures, first at Punta Alta near Bahia Blanca and later elsewhere, Darwin found bones and skulls of the large armadillo-like glyptodont (Fig. 4), the huge ground sloth *Megatherium*, guanacos, and a number of other vertebrate fossils as well as the shells of innumerable mollusks all buried together. These large vertebrates were surely among the most important natural history specimens collected on the voyage, even though his shipmates considered them as "rubbish" and "clutter" as they were laid out on the deck of the *Beagle*. However, many in the ship's crew found natural history intriguing and went with Darwin to help in the discovery and excavation of the fossils. From observations and reading, Darwin realized that the vertebrates for the most part were no longer alive in South America, although most of the marine invertebrates apparently still lived in the near shore waters. He was puzzled by the obvious extinction of the mammals; in this regard, he had the help of the crew who speculated widely. The abundance of fossils of large herbivorous mammals caused Darwin to wonder about the state of the flora present on land when these animals were alive. After examining alternatives, he concluded that the vegetation of the region near Rio Negro, not far from Bahía Blanca, would surely support the large fauna. He also realized the fragmentary nature of the fossil record and that the fossils found so abundantly at Punta Alta were only a partial representation of what must have lived at the time.

FIGURE 4. *Glyptodon asper* collected in South America and now on display in the Galerie de Paléontologie et Anatomie comparée, Paris. (Photo by Michelle Wissig, 2006.)

Darwin also noted the strata entombing the fossils—soft mud, sand, and shells of mollusks. From this evidence together with his observations of the general geology and lithology of the fossil-bearing sedimentary rocks, he concluded that the entire coastal area had been uplifted from the sea, preserving the fossils. To account for the mixture of terrestrial mammals with marine shells, he pictured sediment and bones being swept into a grand embayment by rivers. FitzRoy did not like the idea that the land had risen and favored the Biblical Flood as an explanation for the fossils and

their height above sea level (15–20 feet or so), a point that Darwin did not immediately challenge.

Equally interesting to Darwin were the animals of the Pampas—guanacos, ostriches (rheas), tucotucos, large rodents, and condors and other large birds. Indeed, he spent a good deal of time watching and interacting with many of them. For example, he was quite interested in the behavior of the guanacos (Fig. 5A) and discovered that if he laid down with his extremities in the air, the animals would come to investigate close enough for him to shoot one. He puzzled over the peculiar habit of the guanacos depositing their excrement in large, wide piles of pellets (Fig. 5B). Condors were common on the Pampas then and were hunted and trapped by the people. Darwin also shot one that was sent back to England. Indeed, the ship's crew including Darwin shot a wide variety of animals for eating, as they lived off the land and sea. FitzRoy even acquired a puma, which was skinned and eaten. Food acquisition was, naturally, important to the crew of *Beagle* and it was not always forthcoming. Indeed, sometimes food ran low: "We breakfasted on some small birds and two gulls, and a large hawk which was found dead on the beach. Our dinner was not much better, as it consisted in a fish left by the tide and the bones of the meat . . . ." (Stansbury 1977:93.)

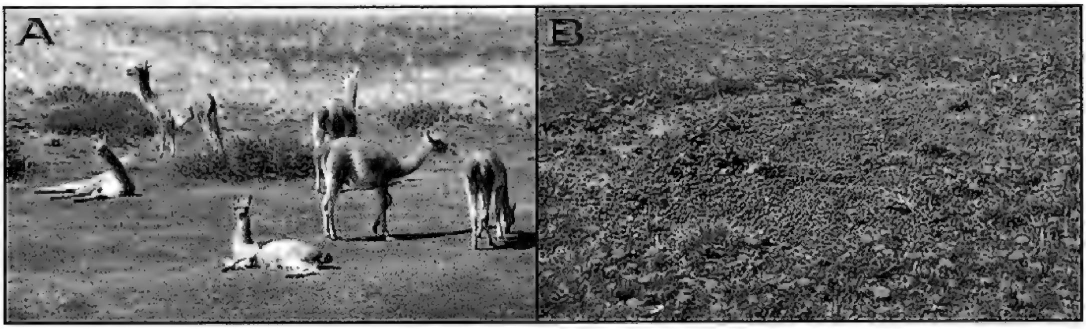

FIGURE 5. Guanacos. A. These animals were common on the Pampas and Darwin was fascinated by them. In his journals, he wrote a number of observations about them, concluding that they were the dominant animal on the plains. Here a group of them relax and graze on grass. B. Guanacos, Darwin noted, have a peculiar habit of repeatedly excreting their dung in large heaps. Darwin found a large quantity in a single place that measured eight feet in diameter. The heap shown here measures nine feet across. (Photos by Jere H. Lipps, 2008.)

Gauchos and Indians were frequently encountered on the Pampas. Darwin took delight in riding with the gauchos and learning about their habits, in particular the hunting technique of throwing the bolas (three stone balls attached together at a central point) to entangle the feet of birds and mammals. For the most part, the Indians kept away from other people on the Pampas because Argentine troops under the command of General Rosas were hunting and exterminating them, a process that horrified Darwin. Nevertheless they posed a danger to small groups. Because of this possibility, Darwin sought the help of Rosas in making his way from Patagones and Bahía Blanca to Buenos Aires on the *Beagle's* second trip south. Six gauchos accompanied him to Buenos Aires.

Upon his return to Montevideo in the spring, about mid-November, 1832, Darwin wrote in a letter to Henslow, mainly concerning his collections and shipping but also about the uncertain future, "On board the ship, everything goes on as well as possible, the only drawback is the fearful length of time between this & day of our return. I do not see any limits to it:— one year is nearly completed & the second will be so before we even leave the East coast of S America.— And then our voyage may be said to have commenced.— I know not, how I shall be able to endure it." (Burkhardt 2008:172.) Perhaps Darwin was a bit homesick since he followed this thought with reference to all the happy hours he spent at Shrewsbury and Cambridge. Little did he know that he still had four more years of surveying, collecting and geologizing on board *Beagle*.

The Islands of Southern South America, December, 1832–April, 1833

The southern part of South America from Strait of Magellan south to Cape Horn consists of many islands of different sizes, nearly all of them parts of the continent that were isolated during the past glaciations and sea level rise, except for the Falkland Islands. They are part of a separate minor continental piece separated from Africa during the fragmentation of Gondwana. Because FitzRoy had to survey the entire region, return the Fuegians and set up a mission, as well as visiting the Falkland Islands, *Beagle* spent more time in these places together (Fig. 2 [10, 11]) than anywhere else the *Beagle* worked. By December 16, 1832, the ship's crew could see fires on the shore of Tierra del Fuego and the natives running along the cliffs. The weather interfered with FitzRoy's objectives, forcing *Beagle* far south of Cape Horn for some time. Nevertheless, *Beagle* or its whaleboats and yawl sailed among this archipelago for 75 days (Figs. 6–7), traversing the Beagle Channel twice, once in each direction, as well as exploring unknown islands.

FIGURE 6. The Beagle Channel. Named by Captain FitzRoy for his ship on the first cruise of the *Beagle*, it is spectacular and well-known for a number of glaciers and high peaks in the Cordillera, including Cerro Darwin, also named by FitzRoy but on the second voyage, for his unofficial naturalist and companion. Although Darwin saw many glaciers in Tierra del Fuego and southwestern Chile, he made nothing of them as a major geologic factor in the landscape. (Photo by Jere H. Lipps, 1983.)

The western and southern parts of the archipelago were largely igneous and metamorphic rock with trends similar to those of the Andes. In the north eastern part were sedimentary rocks identical to those in Patagonia. Although his evidence was very incomplete and he knew nothing of tectonics, his general conclusions have remained more or less valid up to the present day. He did not always get it right however. He seemed oblivious to the work of glaciers on the land although he accepted Lyell's observation that icebergs could float erratic boulders out to sea. At Bahia San Sebastian in Tierra del Fuego, he observed erratics both in the sea and higher on the slopes above the sea. Interpreting these, as Lyell would, he proposed not only that they had been carried by icebergs but that the coast must have risen since their deposition. These boulder trains actually formed by rocks falling by landslide and avalanche onto glaciers that then carried them across Tierra del Fuego and deposited them both in the sea and on the land (Evenson et al. 2009).

FIGURE 7. H.M.S. *Beagle* at Murray Narrows in the Beagle Channel, Tierra del Fuego, in early 1834. The watercolor painting is by Conrad Martens, the artist who accompanied the ship for a year from Montevideo (July 1833) to Valparaiso (July 1834), where he was forced to leave because the Admiralty would not pay additional expenses incurred on the voyage.

Darwin observed the biology too, and he made notes on the birds, insects, marine inverte-

brates, and the *Nothofagus* forests (Fig. 8), dealt with a broader range of conclusions, including some about the behaviors and associations of the animals and of the plants. His observations of the penguins and ostriches (rheas) led him to make comparisons of the life styles of the two birds that he retained even in the *Origin of Species.* He was not impressed with the people, whom he characterized as "miserable creatures, stunted in their growth, their hideous faces daubed with white paint & quite naked" (Darwin 1845:213); and later he would refer them to the lowest rung of all the peoples he met on *Beagle's* voyage, a rather characteristic Eurocentric view at the time but one no longer accepted.

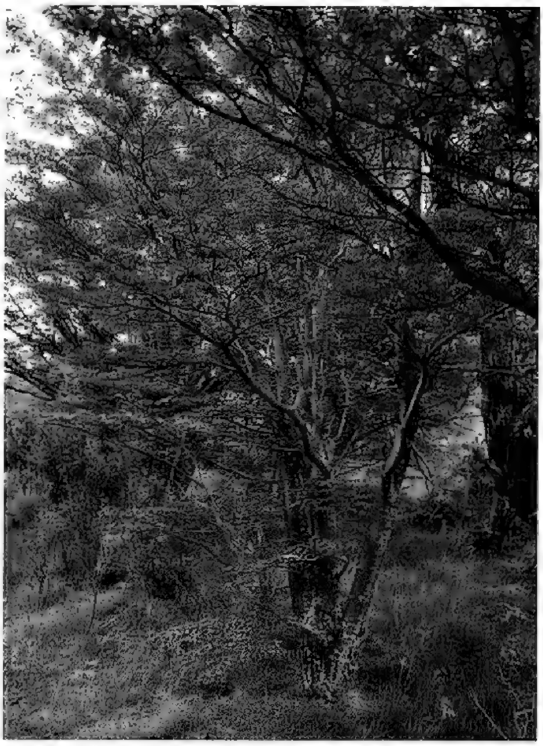

FIGURE 8. *Nothofagus antarctica* forest, typical of southern South America, intrigued Charles Darwin. He wrote no notes on botany because he felt he knew little scientific details about plants although he collected many of them—weeds, seeds, and native vegetation—and commented on them in his personal notes and letters. (Photo by Jere H. Lipps, 2008.)

The *Beagle* set sail for the Falkland Islands (Fig. 2 [10]; Fig. 9) on February 26, 1833, in order to survey East Falkland Island and Berkeley Sound. Darwin was surprised to learn that England had just declared the Falkland Islands its own possession. FitzRoy was to show the flag and inspect the small English station in the Sound while Darwin explored to the southwest. In addition, the ship needed replenishment and repair. This visit to the Falkland Islands lasted for little over a month, from March 1 to April 6 and was the first of two visits *Beagle* would make there. A year later from March to April 1834 *Beagle* would return to complete the work FitzRoy had started in early 1833. In between these times, the ship returned to the east coast of South America to continue surveying and to sail south down the Straits of Magellan before turning back to exit the Strait, and then to explore the eastern and southern (again) coast of Tierra del Fuego. *Beagle* spent her time in Berkeley Sound anchored near the English settlement of Port Luis, while FitzRoy had to deal with a host of problems — the destruction of British property by American whalers, the islands'

FIGURE 9. Port Stanley, Falkland Islands, soon after the end of the 1982 Falkland Islands War. Darwin spent 10 weeks on two different occasions working on the geology of East Falkland Island by traversing from Port Lewis far to the west. He would be unable to do that now, because mine fields remain from the 1982 Falkland Islands War. In 1983, the results of the war had overtaken Port Stanley, which was surrounded by mine fields. (Photo by Jere H. Lipps, 1983.)

sovereignty, shipwrecked French sailors, and mistrust and murder among the inhabitants of the Falklands. He also had to finish his survey of the area. Darwin, on the other hand, spent more time (10 weeks) studying the area west of Port Luis than he had at any other place on the voyage. He was not happy there, but he kept working on the geology, collecting marine and terrestrial life and observing the domesticated animals of Berkeley Sound. Detailed geologic notes and cross sections showing folded strata were produced and invertebrate fossils of an ancient age and quite different environment were collected. Darwin examined the "stone runs" made of angular rocks ranging from a few cm to m in size arranged in long, narrow lineaments in the valleys. Darwin saw clear evidence of catastrophe in geology yet he still held his gradualist Lyellian views. His comparative approaches to biology continued, for example when he noted that the extremely abundant kelp forests of the Falklands were similar to those of Tierra del Fuego and, in terms of abundance, to the tropical rain forests he had seen in tropical South America.

Western South America, from Patagonia to Callao, June, 1834 to September, 1835

FitzRoy finished the work in the Falklands in April 1834, and took the *Beagle* to the coast of Argentina at Rio Santa Cruz just north of the Strait of Magellan, and in mid-May turned back into the Strait to emerge at the Pacific Ocean on 11 June 1834. In the Austral winter, *Beagle* struggled north among the islands of southwestern South America. *Beagle's* passage was rough through the Archipelago de los Chonos to Chiloé Island, Chile (Fig. 2 [13]). The ship at last put ashore at San Carlos for the first time on 28 June 1834. FitzRoy stayed only two weeks at San Carlos, while Darwin explored the northern reaches of the island. Then FitzRoy headed north to Valparaiso to present the ship's papers and to gain permission from authorities in Santiago to survey coastal Chile. *Beagle* remained in the central part of Chile for the winter resupplying and repairing. As *Beagle* surveyed the region, Darwin climbed from Valparaiso past Santiago to the crest of the Andes where he spent time examining rocks and collecting specimens. In November and December 1834, *Beagle* returned to Chiloé and the Chonos Archipelago for surveying in those complex areas. As before, the ship stopped at San Carlos on the north end of Chiloé. Darwin and some of the ship's crew used small boats to sail along the coast to the central part of the island and trekked overland even as far as the west coast on the more exposed Pacific side. The crew and Darwin disliked the overcast and depressing weather they continually encountered, although the temperate rainforests supported by that kind of weather were impressive to Darwin. Darwin was again engaged closely in trying to decipher the geology of the island and relate it to the Andes (Fig. 10) and other parts of Chile he had already seen. In addition to the forests, he studied the Chiloé fox and other terrestrial and marine animals and the people living there. Although Chiloé was part of Chile, it was not secure, thus creating tensions among the population. Nevertheless, Darwin considered Chiloé a fine island and his recollections of Chiloé lasted the rest of his life, perhaps even more so than those from the Galápagos, and he used them in his books and correspondence.

During January 1835, *Beagle* went further south to survey the Chonos Archipelago, before going back in February and March to Chiloé for a third time to complete surveying there. In the Chonos, thick vegetation covered the islands (Fig. 11) so thoroughly that only the intertidal rocks were exposed, making geologizing impossible. Darwin tried to link what he saw there with the geology of other places, but with little success. As usual, he collected a variety of specimens, including a strange barnacle that later proved to be a new order. Unpacking specimens in October 1846, Darwin together with Joseph Hooker discussed this new type of barnacle, and vowed to write a paper on it. This then led to his long study of the barnacles and his monograph on Cirripedia. Evidence of sea level changes were present on the western islands, and like in Argentina, he attributed

this to the rise of the land and of active volcanism in the Andes that were easily visible from the islands and the sea (Fig. 10).

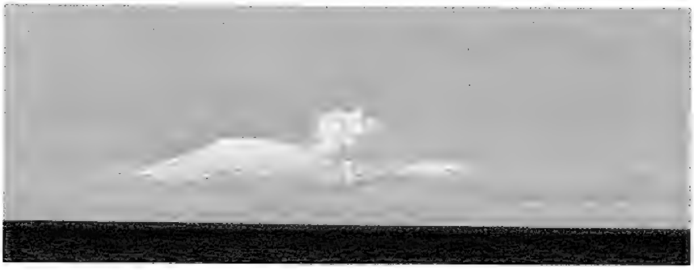

FIGURE 10. Andean volcanoes stand high and frequently erupt, and they were easily seen from the *Beagle* as it sailed through the Gulf of Ancud and Corcovado between the Andes on the east and Isla Chiloé on the west. During the times the *Beagle* passed through the Gulf, Volcan Osorno was erupting. Here Volcan Chaitan erupts in 2008. (Photo by Jere H. Lipps, 2008.)

FIGURE 11. The Chonos Archipelago. Islands and the continental shoreline were and still are covered in such thick, thorny brush that Charles Darwin was unable to do any geologizing except along the very limited intertidal, hindering his geologic interpretations of this part of southern Chile. (Photo by Jere H. Lipps, 2008.)

Beagle left Chiloé on February 5 for more northerly parts of South America, arriving at Valdivia (Fig. 2 [15]) three days later. The town was "a straggling village of wooden houses" (Stansbury 1977:223), according to FitzRoy, with only one stone building, the church. On February 20, a violent earthquake hit the small town, doing little damage to these wooden structures but shaking everything very strongly. Darwin was lying in the forest near town resting and estimated that the earthquake lasted two minutes. From March 4 to 6, 1835, the ship was anchored in the Harbor of Talcuhano, and Darwin had the opportunity to study the effects of the earthquake on the harbor and Concepciòn. Concepciòn was devastated, with hardly a building left standing. Darwin reported to Caroline, his sister, that "It is the most awful spectacle I have ever beheld." Indeed, at the time he ranked it as one of the three most interesting subjects he had seen since leaving England, the other two being tropical vegetation and Fuegian "savages". Geologically, the earthquake confirmed in Darwin's mind Charles Lyell's idea that mountains were built by slow incremental increases in elevation—that Darwin saw first hand with the six foot upward displacement by this earthquake.

From March to September, the *Beagle* made its way up the west coast of South America, staying or working at places long enough for Darwin to explore far inland. At Valparaiso (Fig. 2 [16]), Darwin left the ship to explore the Andes. After crossing the mountains on March 21 through a pass 19,000 feet high, he descended admiring the views of the Pampas that he had previously studied. He arrived in Mendoza, Argentina, his farthest point east, on March 23d. The geology of the mountains thrilled him as he tried to understand the juxtaposition of many different rock types and geologic structures. On the way back over the Andes he found fossil plants and marine mollusks, including oysters, snails, and ammonites at an elevation of over 12–13,000 feet, a fact that he tried to reconcile with Lyell's ideas. Obviously the limestone containing these mollusks confirmed that the Andes had at sometime in the past risen from the sea. The earth's crust was not stable and changed in places significantly. He had seen and felt the evidence of that uplift. After seven months

of sailing along the coast and mostly climbing the mountains on his expeditions, Darwin rejoined the *Beagle* for the trip north to Callao, Peru (Fig. 2 [17]), arriving on July 19. Darwin spent the next few weeks exploring the nearby areas. He found evidence of a huge earthquake and tsunami that had occurred in 1746, which he believed must have been stronger than the one the ship's crew experienced at Valdiz; these observations continued to support his views of the uplift of the Andes, as did terraces along the coast that contained marine mollusks. His last stop was five days in Lima, a city which Darwin thought had been quite splendid, but which was in a state of disrepair and filth left on the streets. Darwin joined *Beagle*, fully resupplied for its Pacific passage, at Callao and he, FitzRoy and *Beagle* departed for the Galápagos Islands on September 7, 1835.

The Pacific and Indian Oceans and, finally, Home September, 1835 to October, 1836

The crew was weary of sailing and of the ship by September 15, 1835, when the *Beagle* arrived at Galápagos (Fig. 2 [18]). Darwin anticipated the Galápagos as a place inhabited by strange animals and pierced by volcanoes everywhere. The islands would not disappoint. Darwin, having departed England well-schooled in collecting, shooting and geology, had put these to practical use during the previous four years; now he was truly an expert practical natural historian and geologist. His appreciation of the tropical and temperate vegetation of South America contrasted with the cactus of Galápagos, his ideas about the rising of the land in recent times, of the volcanism observed in the Andes, of the fossils he had seen on the Pampas and in the Andes, and of the wide variety of invertebrates fitted Darwin with a background of contrasts for the Galápagos. He felt the islands were a world of their own, but built in relatively recent times and populated by a set of animals and plants derived from South America itself. He understood the varieties of similar animals as having been "created" on separate islands, but he still did not have enough information and analyses to understand that Galápagos demonstrated evolution, as he would explain it by natural selection 23 years after the *Beagle* left the islands.

Although FitzRoy launched smaller boats to increase his survey of all of the islands, Darwin remained chiefly on *Beagle* as it moved for five weeks among the islands. He could see 12 of the major islands from the ship or in person, but spent only 19 days or parts of days ashore on only four of the islands (Fig. 12). He did not like the Galápagos very much because it was too hot and barren, nor did he achieve any great insights at the time of his visit. He was awed by the evidence of the very recent volcanic activity, and worried about the giant tortoises and their future given the intense predation on them by ships' crews, including that of *Beagle*. Although Darwin was impressed by the volcanism and low diversity of the fauna and flora, he still made large collections that served him and others well later. These included examples of the finches and other birds, tortoise shells, mollusks, insects, fish, plants, and rocks. Many of these were studied by others, such as John Gould, who later corresponded with Darwin about their significance. Once back in England where he could study his notes and specimens and consult with specialists like Gould, did he begin to formulate his theory of evolution. Unlike most other places he visited, Galápagos had no native population for Darwin to study. The only humans Darwin met were from among the 200 or so Ecuadorian prisoners kept on San Cristobal.

Beagle left the Galápagos for the Society Islands, and passing through the Tuamotus, Darwin could see the low atolls from the deck of the ship. These were the first atolls he ever saw. Finally anchoring at Tahiti in Matavai Bay as British ships had always done, on November 15, FitzRoy set up his magnetic and astronomical measuring equipment on adjacent Point Venus, used in 1768 by Cook for his observations of the transit of Venus. This gave Darwin time to climb the slopes of

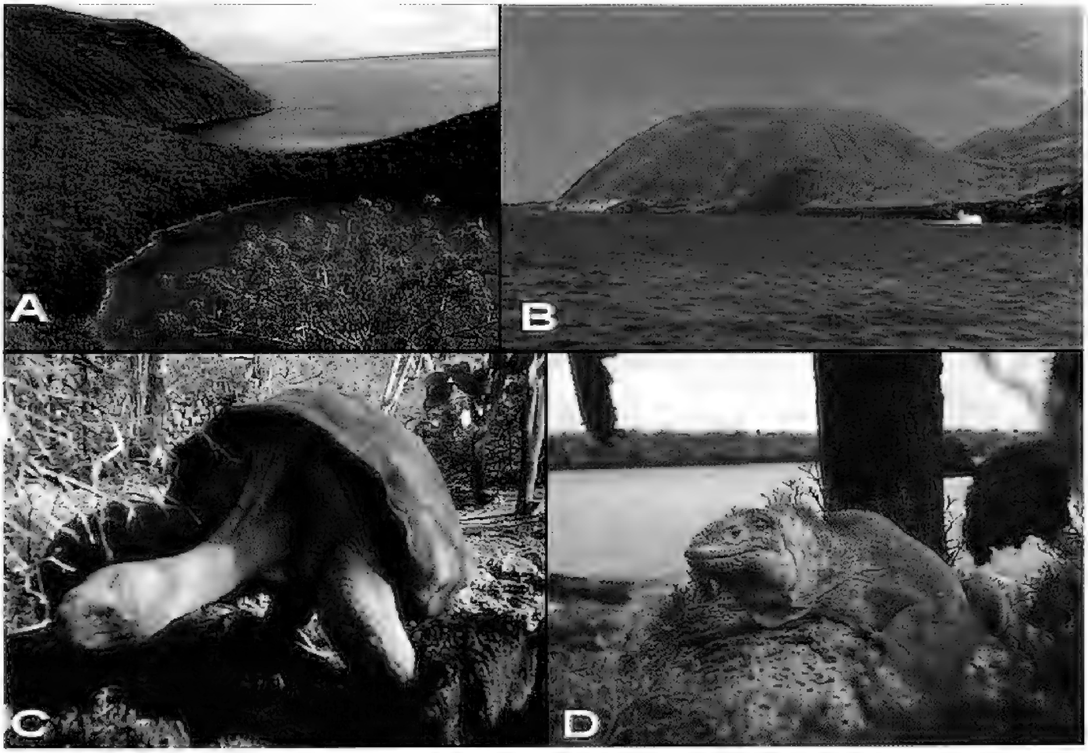

FIGURE 12. Darwin's view of the Galápagos Islands. Darwin saw the Galápagos as a series of young volcanoes on which unusual varieties of organisms had later developed. He visited Tagus Cove and Crater (A) and saw well-formed volcanic cones (B) and other confirming evidence of geologic youth. He collected many animals and, like all visitors to the islands, was especially taken with the giant tortoises (C) and the land iguanas (D), of which he said: "they are ugly animals" with a "singularly stupid appearance" but "when cooked, yield a white meat.". (Photos by Jere H. Lipps, 1982.)

Tahiti high enough (above 800 m) to see the nearby island of Eimeo, now known as Moorea. In this view of Moorea he saw a picture in a frame, the frame being the reef surrounding the island, the mat was the smooth lagoon between the reef and the island, and the picture was the island itself (Fig. 13). He could also see in his mind's eye the sequence of islands that he had seen from the ship in both the tropical Atlantic and Pacific — the fringing reefs that grow next to an island's shore were the first step followed by a barrier reef farther offshore as the island submerged and corals continued to grow, and finally an atoll formed as the island submerged below the surface of the sea leaving only a ring of growing coral. To support his idea, he studied the details of the reefs at Matavai by wading and canoeing over them. He determined that the corals grew best in the upper 120 feet of the ocean and not as well below. The seaward edge of the reefs, he discovered by sounding, fell away sharply into much deeper water. His descriptions were accurate and his conclusions well drawn. Every coral island could be placed into this grand interaction of two processes: volcano submergence and the continued growth of corals to form fringing, barrier and atoll reefs. Inspired by his theory, Darwin wrote a manuscript about it in the month after *Beagle* left Tahiti. The volcanic rocks of Tahiti were well weathered, he noted, and from that he concluded that the island had been active long ago, much longer than at the Galápagos where the rocks were almost everywhere fresh and volcanoes were active. The Tahitians impressed him because of their happy and generally quite religious life style. In his scheme of humanity, he would place these people well above the Fuegians who lacked proper clothing, tools and houses, although he said little about the

lack of dress of Tahitian women. FitzRoy and Darwin discussed this for some time and later on the voyage wrote a paper together on them. Queen Pomare visited the *Beagle*.

Beagle stayed at Tahiti for 11 days and then set sail for New Zealand's Bay of Islands (Fig. 2 [19]) on North Island, another place in FitzRoy's chain of island measurements. As the *Beagle* had now been gone from England well beyond the two years planned, the voyage quickened and surveying work was less extensive. As he had previously stated, Darwin wrote to his sister Caroline again to tell of his own weariness with the voyage: "For the last year, I have been wishing to return & have uttered my wishes in no gentle murmurs; But now I feel inclined to keep up one steady growl from morning to night", a view shared by most of the crew. Thus *Beagle* anchored for only seven days in the Bay of Islands, which was filled with whalers and seamen from other countries. This would be the only place Darwin visited in New Zealand. He saw Maoris and what he regarded as their lowly life style, adding yet another rung to his ladder of human advancement. He thought the missionaries did good work among the Maoris by raising their expectations. Darwin was not too impressed by New Zealand.

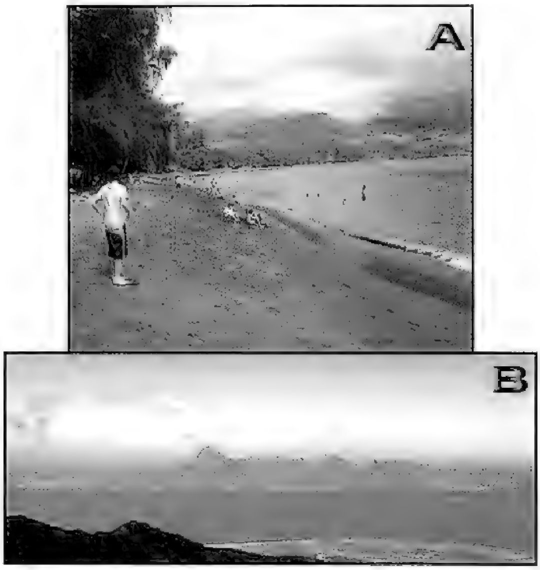

FIGURE 13. Tahiti, Society Islands. Darwin climbed from Matavai Bay (A) to over 800 m on Tahiti. From there he could look across the 20 km to Eimeo (now Moorea) to see the island (B) "like a picture in a frame", with the barrier reef the frame, the smooth lagoon the mat, and the island itself the picture. (Photos A by Jere H. Lipps, 2002; B by Frank Murphy.)

Twelve days later (January 12, 1836) the ship arrived in Australia for restocking of food and supplies. *Beagle* would spend a total of 37 days at Port Jackson (now Sydney) (Fig. 14), New South Wales, Hobart Town, Tasmania, and King George's Sound, Western Australia (Fig. 2 [20–23]). At Port Jackson, Darwin, after a short trip to the outskirts of the town, found that the fauna and flora of Australia was quite different from any other previous places he had visited; nothing could compare with the eucalyptus forests, marsupials and the platypus. Yet he did find a similarity between an ant lion he watched in Australia and those of England. Biogeography was becoming a central tool for understanding evolution. Even in 1836, fire was a prevalent feature of the landscape. He again recorded the major geological features he saw. Sydney, Darwin declared, "might be called a city" (Darwin 1845:446), a view that would be

FIGURE 14. Modern Sydney. Darwin thought "Sydney might be a city" when he was there, but he'd have no doubts now. He would not recognize the place now with its many buildings surrounding the harbor and over four million residents. (Photo by Jere H. Lipps, 1977.)

confirmed if he visited the place today. Eighteen days after arriving at Port Jackson, *Beagle* proceeded on to Tasmania (Fig. 15). At Hobart, the capital of Tasmania, Darwin studied the geology, observed the native people, climbed Mt. Wellington to see the spectacular large eucalyptus trees and geology, and collected organisms. Again he dwelt on the geology, in particular his discovery of some "Devonian or late Carboniferous" fossils (Darwin 1845:448), and the evidence of possible former sea levels and uplift of the land. He compared the local geology to that he saw in New South Wales, using his comparative approach to try to understand the rock types and sequences he described. Again he was interested in the people, this time the conflict between the Aboriginals and the Europeans. The Aboriginals were losing the battle with Europeans, and Darwin felt that the native population would become extinct unless they were separated from the Europeans and removed to a remote area. Eventually the Aboriginals did become locally extinct, as Darwin predicted. Ten days after arriving, *Beagle* left Hobart for Port Williams on Australia's south western coast. Darwin found Port Williams the most "dull and uninteresting time"(Darwin 1845:449) of the entire voyage. Yet he also found the sparse plants, such as the grass tree, and the smooth domes of granite penetrated by numerous veins interesting. An Aborigine group called the "White Cockatoo" men danced often imitating emus or kangaroos for the crew of the *Beagle*. Darwin disliked the dancing: "all moving in hideous harmony, formed a perfect display of a festival amongst the lowest barbarians" (Darwin 1845:451). Overall, Darwin was not impressed—"he who thinks with me will never wish to walk again in so uninviting a country". Indeed, he did not find Australia in general appealing and thought the idea of being served by convicts repulsive. "Farewell, Australia! You are a rising child, and doubtless some day will reign a great princess in the South: but you are too great and ambitious for affection, yet not great enough for respect. I leave your shores without sorrow or regret."

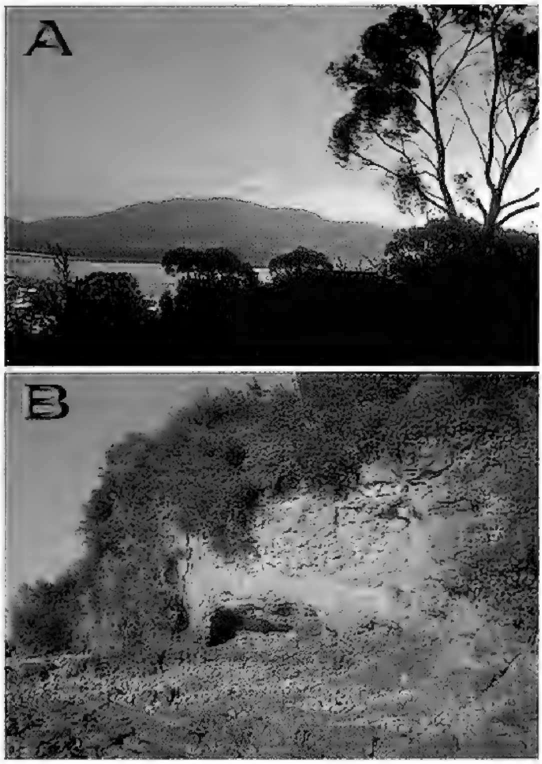

FIGURE 15. Hobart Town, Tasmania. Charles Darwin walked through the town (modern population ~1/2 million) and nearby areas. He spent much of his time here doing geology, although he did not neglect insects (especially beetles), lizards, birds, fungi, and others. Darwin climbed Mount Wellington (A) twice, once failing to get to the top, to inspect the rocks. On one of his several walks, in a cliff, now known as Charles Darwin Cliff (B) south of Blinking Billy Point, he found two submarine lava flows separated by a clay layer. From this he inferred that a volcano had been active in the Tertiary very nearby, a rather astute conclusion for the time, but one that has been confirmed by modern work. (Photos by Roman Leslie of Hobart.)

Although Darwin saw atolls on the way to Tahiti and he correctly surmised their origin, he had never actually set foot on one. As part of the voyage's original plan, Cocos Keeling Islands, lying nearly 2000 km northwest of Perth, Australia, was suggested to FitzRoy by the Admiralty as a place to determine their exact position. The position of *Beagle* far to the south prompted FitzRoy to write to the Admiralty that he would take the ship directly across the Indian Ocean, then to England, as sailing to the Cocos Keeling Islands would increase the time and distance of the voyage consider-

ably. Darwin, however, was anxious to visit an atoll and that may have influenced FitzRoy to change course and set sails for the atoll, much to Darwin's delight.

The Cocos Keeling Islands (Fig. 2 [23]) consist of two atolls and, like most atolls, they have many small islets on the coral rims. From April 1 to 12 *Beagle* surveyed the islands and established their positions while Darwin visited five of the small islands by boat. A European and Malay population lived on the main island. Darwin was curious about the vegetation, beaches with pumice and plant debris tossed up by waves, the spiders, insects and large coconut crabs (*Birgus latro*), the lagoon with its variety of marine animals including many giant clams (*Tridacna*), and the communities of people. He collected much of the depauperate flora and fauna; thinking that he had specimens of every plant (20) save two that existed as single trees whose seed were likely tossed ashore by the waves. *Pemphis acidula* was the first tree to occupy newly formed islets on the atolls and it lived closest to the outer surf, he noted. Darwin's theory of atoll formation was most likely confirmed for him given what he saw at Cocos Keeling. Perhaps he wondered how far the volcano, which supported this atoll, was below his feet. He was quite happy and seemed to enjoy his visit to the atolls.

Continuing the homeward trip, *Beagle* next anchored at Port Louis on the northern side of Mauritius (Fig. 2 [24]). Although Darwin spent much time walking about town and watching the society at work, he also examined the relationship of the coral reefs to the volcanic rocks of the island, the apparent recent elevation of the land, and the nature of volcanic structures observed in the interior; he was able to place this island into his theory of reefs through comparisons to the other islands he had visited. Darwin did not collect much, but he did find a frog, which puzzled him since amphibians were nonexistent on islands, presumably because they could not cross salt water. Later, the frog was discovered to have been introduced.

From Mauritius, FitzRoy steered to Cape of Good Hope where the ship stayed from May 31 to June 15, 1836. This gave Darwin a chance to travel by carriage to Cape Town which he explored. He also was curious about the geology as revealed in the spectacular Lion's Head, Table Mountain and other sites in the vicinity of Cape Town. He recorded schists and sandstones overlying granite. These sandstones, part of the Permo-Triassic Karoo Formation, were similar to sandstones on granite in Brazil described earlier by others. It now seems remarkable that Darwin made the connection between the sandstones in South Africa and Brazil, for today we know that they are the same rocks split by the plate tectonic motions separating Africa and South America. Sir John Herschel, the well-known astronomer, was put in charge of the Royal Observatory at Cape Town in 1833. Darwin, when in Cape Town, visited with Herschel about natural history, the formation of species and geology. When Darwin died in 1882, he was interred at Westminster Abbey next to Herschel.

Beagle returned to the Atlantic on June 15. FitzRoy sailed to St. Helena, Ascension, Bahia and the Cape Verde Islands again, and, finally, Terceira in the Azores (Fig. 2 [26, 27, 6, 3, 28]). St. Helena and Ascension are hot-spot volcanoes close to the Mid-Atlantic Ridge made chiefly of basalt. Darwin thought these islands and St. Jago, which he had visited early in the voyage, were rising because of volcanism while erosion was lowering them. He concluded that Ascension was much younger than St. Helena based on the fresher appearance of the lava flows. In fact, later geologic studies have confirmed this. FitzRoy had been worried about uncertainties in his measurements made at Bahia, Brazil, in 1832, so he determined that *Beagle* should return to that area and make new ones. Darwin and the crew were unhappy heading southwesterly rather than north because they wanted to head home. The work took from August 1 to 17 with stops at Bahia and Pernambuco. Disappointed by the change in plans, Darwin nevertheless took excursions inland examining the geology and caught organisms for his collection at different depths off the coast. The *Beagle* stopped at St. Jago in the Cape Verde Islands again on September 4, remaining there for five days.

She arrived at Terceira in the Azores, staying there from September 20 to 24 to complete FitzRoy's measurements on the meridians. Darwin, although less than enthusiastic about the short stay, made three excursions on the island, one to see an active crater in the center of the island that turned out to be merely fumaroles. From his observations, he decided that lava flowed from the center of the island outwards toward the shores.

In the evening of October 2 , 1836, after nearly 5 years, the *Beagle* tied up at Falmouth, England. Darwin immediately left for his home in Shrewsbury arriving two nights later. Darwin never again left the British Isles.

Besides Galápagos

Charles Darwin, in under just five years on the voyage of the *Beagle*, made discoveries that would change the world. In the 1737 days on the *Beagle* or traveling inland from the sea by foot, horseback or carriage, he saw new animals, plants, people, and geology that influenced him for the rest of his life. Well trained in natural history and geology by his own interests as a child and his experiences at Edinburgh and Cambridge Universities, he came on board the *Beagle* as an unofficial naturalist and guest of Captain Robert FitzRoy. From this training he built his huge scientific knowledge directly from his observations of the biology and geology studied on the many islands, three continents (South America, Australia and Africa) and three oceans on the voyage. Starting chiefly as a collector of organisms and rocks, his experiences in natural history and geology led quickly to attempts to understand the processes by which islands, mountains, fossils, and all the organisms he collected came to be. He developed a comparative method he used to explain phenomena and objects far beyond their mere description. Comparisons of observations he and others had made to new observations resulted in a rapid understanding of the processes that were involved. This comparative research style was used throughout the voyage. Darwin referred to "struggles" between various natural elements. This concept developed early in the voyage and he returned to it often. He referred to the struggle of native species to resist those recently introduced, of corals to resist waves, of one species in competition with another, and of waves against the shore. He saw volcanic islands, continental islands, very isolated islands, tropical and subpolar islands, and those in close proximity to their neighbors. These, Darwin realized, determined their biotas. Darwin had seen enough during the voyage of the *Beagle* to write many books and articles that changed biology and geology forever.

Most of Darwin's methodology developed before he reached the Galápagos Islands. Indeed, the work done on those islands differed very little from how he approached his studies of the islands in the Atlantic, southeastern Pacific or of eastern and western South America. He arrived at the Galápagos excited to see its volcanic geology and to examine the unusual biota he knew about previously. He had relatively little time on the Galápagos and he had no great insights to their biology. His notebooks reveal little of what would come from Darwin long after the voyage. He had written 80 pages on the geology and 25 pages on the zoology of the islands in just 19 days ashore. But those notes would be later used in conjunction with his specimens and the expertise of specialists to develop his ideas. Much of the Galápagos fame as a laboratory for evolution came from later scientists long after Darwin died. These scientists acknowledged the debt they owed Darwin. The Galápagos are unique, without doubt, but the general phenomena that interested Darwin were apparent to him throughout the voyage. Would Darwin have written his evolutionary ideas without his Galápagos experiences? Most likely, because the fauna and flora, while bizarre and significantly different from others seen elsewhere, were examples of what he understood in general.

Darwin made other more immediate contributions which sometimes involved Galápagos

observations. Geology attracted Darwin's attention more than biology as is apparent in his notes from the voyage of the *Beagle*. He wrote 1383 pages of geological notes and 368 pages of zoological ones and none on botany, as well as another 779 pages of "personal" notes. These were not evenly distributed in time either. This geologic interest started before the voyage began but it certainly manifested itself with the first stop at St. Jago in the Cape Verde Islands. There he declared that he should write a book about the geology of volcanic islands, which he did, and which relied in part on the geology of the Galápagos. However, he developed his theory of atoll formation independently from Galápagos and chiefly from observations on the relationship of corals to volcanic islands that he observed over more than three years in the Atlantic and Pacific Oceans, and later confirmed in the Indian Ocean. The theory of corals growing fast enough to keep up with the submergence of a volcano has since become widely accepted by scientists everywhere but it did not account for the volcano's subsidence. Darwin proposed that because some parts of the earth's crust rose up, like the Andes, other parts must balance that by submerging. While that turned out not to be true, submergence did occur but through mechanisms of plate tectonics that were understood only in the 1960s. The Darwinian view of coral reefs and atolls remains prominent in modern textbooks of biology, geology and oceanography.

Darwin was concerned about the conservation of animals, plants and even people as a result of his observations during the voyage. At the Galápagos, for example, he thought the harvesting of tortoises by ships' crews for food might lead to their extinction. He was concerned even more about the preservation of unique peoples. In Tasmania, Aboriginal people conflicted with Europeans and their population was declining as a result. Based on his other island observations, Darwin believed that the only way to preserve them as a people was to remove them from Tasmania and place them in a locale far from Europeans. Without this move, he predicted that they would go extinct as a pure race, which, indeed, they did less than 40 years later. Darwin knew that invasive species of alien plants and animals to islands caused destruction and extinction of native species. At the Bay of Islands, he saw that many weeds and the common black rat had also been accidentally introduced along with the English plants growing there. The invasive species were regarded as a threat to the native species, especially the black rat which Darwin knew had already eliminated the Polynesian rat. Other cases were known to Darwin as well. Introduced plant species at St. Helena were replacing the natives, and introduced goats demolished much of the vegetation, resulting in the extinction of land snails and probably insects as well. On Ascension, feral cats were a problem, and Darwin condemned them as a plague on the land. He was even aware of the human impact through removal of the trees on the formerly well-forested island.

Much has been made of his time in the Galápagos, but that time should not be emphasized at the expense of the rest of voyage. Darwin's great ideas and books came from the entire voyage as well as the knowledge of other people he knew or read, and of course from his own great mind.

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The Natural History of Hell: The Galápagos Before Darwin

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The Galápagos Island gained a niche within European natural history even before Charles Darwin's 1832-36 voyage aboard the British survey ship *Beagle* that transformed them into a fabled laboratory of evolution. The Spanish bishop Tomàs de Berlanger discovered the uninhabited archipelago in 1532, when his ship became becalmed there on an official voyage from Panama to Peru. He brought back tales of strangely desolate islands with gigantic land tortoises and fearless birds. Gaining favor as a resort for British and Dutch privateers preying on Spanish ships carrying gold and precious metals north from Peru, reports continued to reach Europe about the archipelago's distinctive reptiles and birds. A late 18th Century British expedition led by James Colnett depicted the region as a breeding ground for whales, leading to a rush of whalers to the islands. Small settlements sprang up and the waters became site of skirmishes during the 1812-14 war between the United States and Britain, both of which boasted large whaling fleets. Growing interest in distinctive Galápagos plants and animals also led to stops there before Darwin by Vancouver's Discovery expedition, British botanical collector David Douglas, and Lord Byron on his voyage to Hawaii. Although these explorers and travelers found the native flora and fauna interesting, no one succeeded in explain it until Darwin offered his evolutionary account. Rather than an exhilarating place for evolving new species, the Galápagos struck previous visitors as a damned creation.

From its first discovery in 1835, the Galápagos archipelago seemed like something special. The only question was: was it especially good or especially bad. Outside the polar regions, nearly every island of any size or significance already had people living there when Europeans discovered it. "Discovery" was simply a Western convention to legitimize the conquest of these places in the eyes of other Europeans. The Galápagos stand as one of the few exceptions to this rule. Despite vague Inca legends to the contrary, no one has ever detected any credible evidence that humans lived on these islands before the first European ship entered their waters in 1535.[1] Their virgin state would one day help make the Galápagos Islands especially intriguing to scientists. At the time, it rendered them of little interest to their first discovers, the Spanish. If God made the earth for human habitation, as their religion told them, what could explain an uninhabited place? Fittingly, a Roman Catholic bishop discovered these islands (one of the few times that a church official played such a role) and promptly pronounced them cursed of God. Thereafter, pious Spaniards generally left them alone. That bishop, Fray Thomas de Berlanga, drifted off course on his way to Peru and reported on his find to his monarch in Spain.

[1] Joseph Richard Slevin, "The Galapagos Islands: A History of Their Exploration," *Occasional Papers of the California Academy of Science*, 25 (1959), 11-13; Victor Wolfgang von Hagen, *Ecuador and the Galapagos Islands* (Norman: University of Oklahoma Press, 1949), 177-78.

Berlanga's report damned the archipelago. "I do not think that there is a place where one might sow a bushel of corn, because most of it is full of very big stones," he wrote, "and the earth that there is, is like dross, worthless, because it has not the power of raising a little grass, but only some thistles." The fauna was as wretched as the flora: "many seals, turtles, iguanas, tortoises, many birds like those of Spain, but so silly they do not know how to flee, and many were caught in the hand." God did not make this place for humans, the bishop concluded. "It seems as though some time God had showered stones."[2] Following this report, the Spanish government never attempted to colonize the islands and few other than outlaws and privateers visited them until 1800. Of these, the most important for science was the British gentleman-buccaneer William Dampier, whose 1697 book, *A New Voyage Round the World,* contained passages about the natural history of the Galápagos Islands, which his band of privateers used as a hideout on several occasions. Like Berlanga, Dampier condemned the islands as unfit for human habitation: "4 or 5 of the Eastermost are rocky, barren, and hilly, producing neither Tree, Herb, nor Grass," he wrote.[3] Only the land tortoises and sea turtles, which he recommended as food for hungry sailors, escaped his criticism. Later British and American whalers and naval personnel, who began arriving in increasingly large numbers around 1800, generally expressed similar views of the place. It reflected a particular perspective on nature that dominated Anglo-American science before Darwin.

"In crossing a heath, suppose I pitched my foot against a stone, and were asked how the *stone* came to be there, I might possibly answer, that, for any thing I knew to the contrary, it had laid there forever." So wrote the sometimes Cambridge University lecturer and Anglican cleric William Paley to begin his profoundly influential 1802 treatise, *Natural Theology*. "But suppose that I had found a *watch* upon the ground, and it should be inquired how the watch happened to be in that place." Surely the former answer would not do. "The watch must have had a maker," Paley concluded, "who comprehended its construction, and designed its use."[4]

This most famous passage of English popular science writing resonated in its day because it articulated the view of nature widely held by scientists throughout the English speaking world during the first half of the nineteenth century. At the time, British and American scientists largely viewed nature through the lens of natural theology — expecting and finding evidence of God's existence and character in the world around them. British and American thought mattered for the Galápagos Islands because of the dominant role then played by Britons and Americans in studying the place. (And following general conventions of the time, "Americans" in this context and hereafter refers to people from the United States, not from the Americas generally.) Increasingly during the eighteenth and nineteenth centuries, British and American ships ruled Pacific exploration and commerce — with the Galápagos Islands falling within that domain despite their proximity to South America. Spanish (and later Ecuadorian) sovereignty over the uninhabited archipelago meant little.

The theistic tone of eighteenth and early nineteenth century Anglo-American natural history — a field of science that then broadly incorporated botany, zoology and geology — was fixed in the early 1700s with the publication of John Ray's *The Wisdom of God Manifest in the Works of Creation*. Before writing this classic work, the energetic and influential Ray had laid the foundation for modern natural history in Britain by compiling the first systematic accounts of the kingdom's native plants, fish, mammals and reptiles.

With *The Wisdom of God*, Ray placed a firmly religious stamp on that biological portrait of

[2] Ibid., 15-16.

[3] William Dampier, *A New Voyage Round the World* (London: James Knapton, 1697), 100.

[4] William Paley, *Natural Theology: Or, Evidence of the Existence and Attributes of the Deity, Collected from the Appearance of Nature* (Philadelphia: John F. Watson, 1814 rpt.), 5-6 (emphasis in original).

Britain. This book, Ray wrote in its Preface, would "serve not only to Demonstrate the being of a Deity, but also to illustrate some of his principal Attributes, as namely his Infinite Power and Wisdom" in the "admirable contrivance" of the earth and its beings. Ray specifically portrayed clouds, water, plants, soil and mountains as so providentially distributed "as to render all the Earth habitable" by humans — yet even a casual visit to the Galápagos Islands (or any number of deserts, ice sheets or jungles) would give the lie to such anthropocentric assumptions.[5] If naturalists looked to nature for their theology and that theology placed humans at the center of God's creation, better to ignore places like the Galápagos, which no humans had colonized prior to 1800.

Ray's brand of natural theology made matters even worse for understanding the Galápagos Islands by admitting no change in nature. "By the Works of Creation," he wrote, "I mean the Works created by God at first, and by Him conserved to this Day in the same State and Condition in which they were first made."[6] This definition either excluded the Galápagos from creation altogether or left their ongoing volcanic development inexplicable. If a human-designed watch (with its interlocking gears and functional face) came to symbolize nature for British natural historians after Paley, then it was a timepiece without a date indicator to mark the passing of longer periods than the hour. Despite their preoccupation with the watch metaphor, eighteenth century British natural historians before Darwin, inspired in their work by the doctrines of natural theology, lost track of time. Yet it is the temporal perspective that makes the Galápagos Islands of interest to science. Without a concept of geological or biological change, the archipelago made little sense. It is a common pattern in science: observations not fitting into existing theories are often ignored.[7]

Between the absence of scientific interest in the Galápagos Islands and their apparent lack of economic or strategic importance, the expeditions of exploration that charted the Pacific during the 1700s had largely bypassed the archipelago. The legendary voyages of James Cook offered a case in point. Cook's three expeditions canvassed the Pacific for Britain from 1768 to 1780, looking for everything of scientific, economic or strategic value. They sailed by the Galápagos without stopping.

Assigned to follow up on some of Cook's investigations, George Vancouver (who served on Cook's final voyage) sailed his great ship *Discovery* through the archipelago in 1795 with scarcely more than a puzzled nod. "The interior country exhibited the most shattered, broken, and confused landscape I ever beheld, seemingly as if formed of the mouths of innumerable craters of various heights and different sizes,"[8] Vancouver observed without disembarking. The ship's naturalist, Archibald Menzies, who briefly went ashore on Isabella Island with a small landing party, called it "the most dreary barren and desolate country I ever beheld."[9] Dismissing the archipelago as a "very dreary and unproductive"[10] place, Vancouver promptly departed after the landing party found "neither fuel nor fresh water."[11] But even in Vancouver's day, the rise of deep-ocean whaling began changing the public perception of the Galápagos.

The process began with a report penned by the British navy captain James Colnett, who had

[5] John Ray, *The Wisdom of God Manifested in the Works of Creation* (London: Samuel Smith, 1691), xiv, 60-65 and 135-50 (quotes from xiv, 63).

[6] John Ray, in John C. Greene, *The Death of Adam: Evolution and Its Impact on Western Thought* (Ames: Iowa State University Press, 1959), xii.

[7] For the classic discussion of this trait of science, see Thomas S. Kuhn, *The Structure of Scientific Revolutions*, 2nd ed. (Chicago: University of Chicago Press, 1962), 52-65.

[8] George Vancouver, *A Voyage of Discovery to the North Pacific Ocean and Round the World*, 1791-1795, (London, Hakluyt Society, 1984), IV, 1462.

[9] Ibid., I. 193

[10] Ibid., IV, 1463

[11] Ibid., IV, 1462

served with distinction on Cook's second voyage and was dispatched by the admiralty in search of new, commercially exploitable whaling grounds at the behest of influential London merchants. Colnett began his search in the South Atlantic early in 1793, but by the following spring his quest carried him around the Horn and into Galápagos waters. "Here we cruised till the eighth of April, and saw spermaceti whales in great numbers," Colnett noted in his journal. "I am disposed to believe that we were now at the general rendezvous of the spermaceti whales from the coasts of Mexico, Peru, and the Gulf of Panama, who come here to calve." In support of this conclusion, Colnett reported observing many of these whales "in a state of copulation," an impressive act that neither he nor any of "the oldest whale-fishers, with whom I have conversed" had ever before witnessed. Here was the mother lode of whales![12]

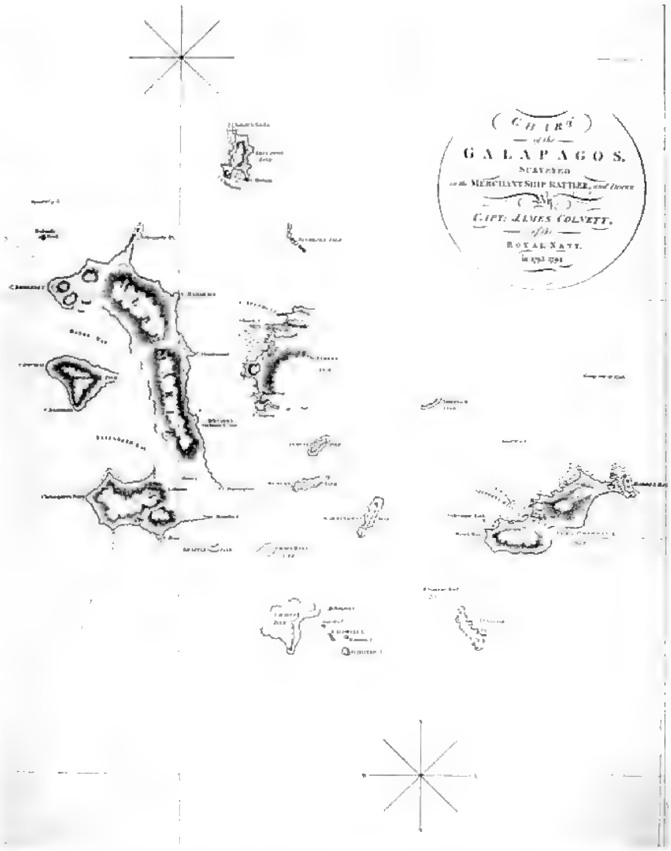

FIGURE 1. Colnett's chart of the Galapagos Islands (1798). (Used by permission of the University of Georgia Libraries.)

Colnett and his crew visited the archipelago twice during their two-year cruise. Their eyes now open to its animal life, they beheld its marvels — perhaps the first people to appreciate them so fully. "In this expedition we saw great numbers of penguins, and three or four hundred seals," Colnett wrote of their stop on one island. "There were also small birds, with a red breast, such as I have seen at the New Hebrides; and others resembling the Java sparrow, in shape and size, but of a black plumage; the male was the darkest, and had a very delightful note."[13] Clearly struggling to relate the local animals to known types from other places, Colnett repeatedly resorted to the superlative. "There is great plenty of every kind of fish that inhabit the tropical Latitudes; mullet, devil-fish, and green turtle were in great abundance," he noted. "But all the luxuries of the sea, yielded to that which the island afforded us in the land tortoise, which in whatever way it was dressed, was considered by all of us as the most delicious food we had ever tasted. The fat of these animals when melted down, was equal to fresh butter."[14] From feasting on these great beasts, Colnett exalted, "all apprehensions of scurvy or any other disease was at an end."[15]

In an age that sought God's divine design and providence everywhere in nature, Colnett began

[12] James Colnett, *A Voyage to the South Atlantic and Round Cape Horn into the Pacific Ocean* (London: W. Bennett, 1798), 146-48.

[13] Ibid., 156.

[14] Ibid., 157-58.

[15] Ibid., 59; Joseph Richard Slevin, "The Galapagos Islands: A History of Their Exploration," *Occasional Papers of the California Academy of Sciences*, 25 (1959), 42.

to see them on the Galápagos as well. Of course a breeding ground for whales stocked with delicious and nutritious tortoises represented a Godsend. The place even offered respite for sailors from the oppressive tropical heat. "In the morning, evening and night, it was below summer heat in England," Colnett marveled. "I consider it as one of the most delightful climates under heaven." Even the lack of fresh water seemed tempered by an abundance of succulent plants. Tortoises sucked water from tree bark, birds drew it from leaves, and in one touching scene of benevolence in nature, sailors "observed an old bird in the act of supplying three young ones with drink, by squeezing the berry of a tree into their mouths."[16] Such complex interactions seemed certain evidence of divine beneficence.

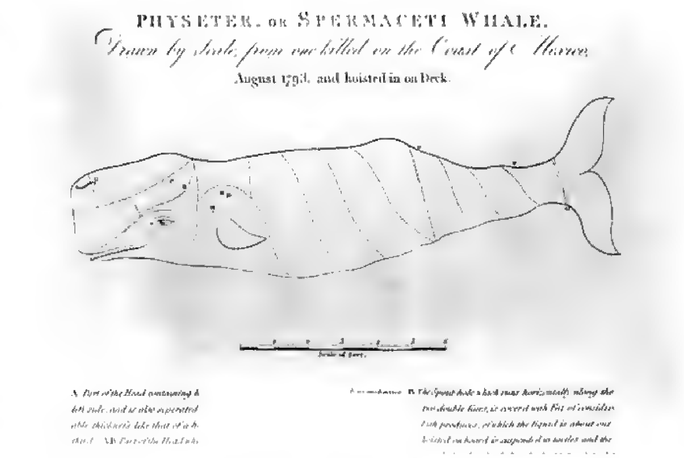

FIGURE 2. Illustration for James Colnett's report on Galapagos whaling (1798). (Used by permission of the University of Georgia Libraries.)

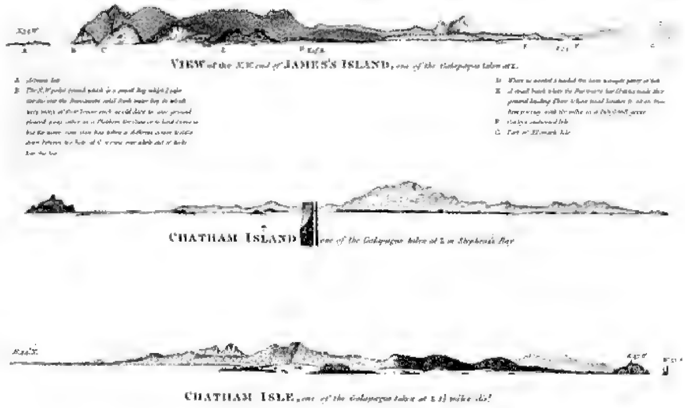

FIGURE 3. Island views of the Galapagos from Colnett's report on whaling (1798). (Used by permission of the University of Georgia Libraries.)

The inhospitality of the islands ultimately darkened Colnett's vision of the place. His second stop at the archipelago coincided with one of its periodic droughts. Rock cavities and hollows that once retained rainwater for human and animal consumption were now dry. The succulents had withered. "An officer and party, whom I sent to travel inland, saw many spots, which had very lately contained fresh water, about which, the land tortoises appeared to be pining in great numbers," Colnett noted. As for the small land birds once seen resourcefully squeezing berries and piercing leaves for water, "on our return, we found great numbers dead in their nests, and some of them almost fledged."[17]

Struggling to come to terms with the place, Colnett ultimately concluded that, at least for whalers, the bounty of the Galápagos's sea life outweighed the bane of its landscape. Perhaps that made the archipelago cognizable even within the constraints of natural theology. Situated amidst breeding grounds for whales, with tortoises to eat and enough seals to "form no inconsiderable addition to the profits of a voyage," Colnett opined, "these isles deserve the attention of British navigators."[18] They received that attention for as long as the South Seas whaling boom continued.

[16] James Colnett, *A Voyage to the South Atlantic and Round Cape Horn into the Pacific Ocean* (London: W. Bennett, 1798), 53, 58.

[17] Ibid., 52-54.

[18] Ibid., 57, 159.

For the next half century, whalers flocked to Galápagos waters. Many came from Great Britain, as Colnett and his sponsors had hoped, but even more from New England. Rivalries sometimes developed between American and British sailors during those years of heightened nationalism between the American Revolution and the War of 1812. Although both sides relied on Colnett's report and chart, the Americans criticized them the most — perhaps to diminish any claim to the place that Colnett's expedition might give to the British. Captain Amasa Delano, who came from the same Massachusetts family that later produced Franklin Delano Roosevelt, exemplified the American side.

Delano visited the Galápagos Islands in 1800 under unusual circumstances. In command of a merchant vessel engaged in the China trade, he stopped there to allow his crew time to recover from scurvy. This gave the able-bodied Delano ample opportunity to explore the surroundings, and his published journal offered some of the best early descriptions of Galápagos reptiles, including the first known report of the lava lizard (noting its "bright vermilion red throat").[19] The islands' giant tortoises received the most attention: Delano's detailed description of their physical characteristics, mating behavior and diet extends for pages. Based on his observation of captured ones, Delano was the first to suggest in print that they survived long periods of drought in the Galápagos environment by consuming stored fat.[20]

Turning to native birds, Delano contributed the most detailed written accounts to date of the brown pelican, the Galápagos dove and the as yet unnamed blue-footed booby. "They resemble the small kind of booby," he observed about this last type, "excepting they are of rather a darker colour on the breast and neck, and their beaks and feet are of a Prussian blue." Delano marveled at their ability to dive for food "from sixty to a hundred yards in the air," adding that they "go into the water with the greatest velocity that can be conceived of, exceeding any thing of the kind that I ever witnessed." Plunging to great depths through the transparent sea, "they glide under water at almost as great a degree of swiftness as when flying in the air."[21]

As in Colnett's journal, however, gloomy reports of the land tempered the glowing accounts of the animals, leaving a hellish overall image. Delano described San Cristobal Island as "mountains of rocks burnt to a cinder." Of Espanola, he wrote, "the surface is burnt stones and sand, with some small shrubby wood growing on it." Isabella's "appearance is like most of the other large islands, a great part of it appearing to have been torn to pieces by volcanos." As if to punctuate the burnt-over aspect of the place, Delano watched one of Isabella's volcanos erupt: He called it "the most extraordinary phenomena . . . that I have ever witnessed in my life." Drought added to the desolation, leading Delano to comment "that it never rained at these islands" and to write them off for human habitation.[22] The great American writer, Herman Melville carried Delano's grim depiction of the Galápagos landscape into his later sketches of the Enchanted Isles. For him, they were an evilly enchanted place.

Melville drew even greater inspiration for his sketches from the next notable island visitor, American navy hero David Porter. At the outbreak of its war with Britain in 1812, the United States government despatched Porter, in command of the frigate *Essex*, to protect American whalers in the South Seas and harass British ships there. This brought him to the Galápagos Islands, where he cruised from April to September, 1813. The *Essex's* total success in its mission, which forced the British admiralty to send a small fleet in pursuit, made Porter's name second only to John Paul Jones in early American navy lore and made his journal an American naval classic that has never

[19] Ibid., 379.
[20] Ibid., 376-77.
[21] Ibid., 380-81.
[22] Ibid., 370-71, 382-83.

gone out of print.[23] It became one of the most significant travel books for awakening readers to the distinctive natural history of the Galápagos Islands, second only to Darwin's *Journal of Researches*.

Gallapagos turtle

FIGURE 4. Galapagos land tortoise from David Porter's *Journal of a Cruise* (1822). (Used by permission of the University of Georgia Libraries.)

Following Colnett, whose published journal and chart he took on the voyage, Porter condemned the Galápagos as uninhabitable. "These islands are all evidently of volcanic production; every mountain and hill is the creation of an extinguished volcano," he observed. "Thousands of smaller fissures, which have burst from their sides, give them the most dreary, desolate, and inhospitable appearance imaginable."[24]

Unlike any of his predecessors, however, Porter did not view the islands' condition as permanent. In the years since Colnet's voyage, the Scottish gentleman-naturalist James Hutton had completed his revolutionary *Theory of the Earth*, which began transforming how science interpreted the development of the earth's features. It built on a generation of fieldwork, mostly by French naturalists, that finally began to recognize the widespread occurrence of volcanic activity and its impact in shaping terrain over time. Rather than a one-time event within the past 10,000 years as suggested by the Genesis account in the Bible, geology became an ongoing process with no vestige of a beginning and no prospect of an end.[25] Although Hutton's views were not widely accepted by contemporary naturalists, they were familiar to British and American readers through John Playfair's 1802 book *Illustrations of the Huttonian Theory of the Earth*.

Porter never mentioned Hutton by name, but Huttonian thinking ran through his interpretation of the Galápagos. As the most volcanically active, the western islands were the newest, Porter reasoned vulcanism must still be pushing them up from below the sea floor. Fernandina Island, which erupted during his visit, "probably owes its origin to no distant period." Its "hills composed of ashes and lava, all apparently fresh, and in most parts destitute of verdure, sufficiently prove that they have not long been thrown from the bowels of the ocean." Returning to Fernandina after its eruption, Porter added that it "appeared to have undergone great changes since our last visit." Several craters had begun spewing forth smoke, as had one crater on nearby Isabella, suggesting to him "a submarine communication between them."[26] Here were ongoing, interconnected geological forces sufficient to shape the earth's features, just as Hutton's theory predicted: No need for a single creative act to do the sculpting.

Porter noted subtle differences as he moved from west to east within the archipelago. He wrote of San Cristobal in the extreme east, "This island, like all the rest, is of volcanic origin, but the rav-

[23] E.g., Herman Melville, "The Encantadas, or Enchanted Isles," in eds. Harrison Hayford, et al., *The Piassa Tales and Other Prose Pieces: 1839-1860* (Evanston: Northwestern University Press, 1987), 143.

[24] David Porter, *Journal of a Cruise* (Annapolis, Md.: Naval Institute Press, 1986), 155 (reprint of 1815 edition noting changes of 1822 edition).

[25] Roy Porter, *The Making of Geology: Earth Science in Britain, 1660-1815* (Cambridge: Cambridge University Press, 1977), 184-215.

[26] Porter, *Journal of a Cruise*, 167, 204-05, 232.

ages appear less recent." Speaking of it and two central ones, Santiago and Floriana, he added, "The soil of these islands, although dry and parched up [due to drought], seems rich and productive; and, were it not for the want of streams of fresh water, they might be rendered of great importance to any commercial nation that would establish a colony on them."[27] Thus soil had appeared with time, again in accord with Hutton's theory. Given more time, Porter suggested, the light volcanic soil would compact sufficiently to hold water, permitting "springs or streams of water, for the support of animal life."[28] Although all of the islands remained uninhabitable by humans, he told of four goats from his ship escaping onto Santiago Island and apparently surviving in its moist highlands. Porter also related the story of a marooned sailor named Patrick Watkins who survived for years on Floriana Island, and managed to grow some vegetables there. "We have seen, from what Pat has effected, that potatoes, pumpkins, &c., may be raised," Porter commented, "and with proper industry the state of these islands might be much improved." They remained too new for now, he acknowledged, but "time, no doubt, will order it otherwise; and many centuries hence may see the Gallapagos as thickly inhabited by the human species as any other part of the world."[29]

With Porter and Colnett spiking interest in the archipelago, the Galápagos were primed for Darwin's arrival aboard the British survey ship *Beagle* in 1835. By then, on the heels of Porter, the islands' Ecuadorian overlords had occupied the archipelago and began making it a habitat for humans, which was how Darwin found it, and how we still find it today: No longer damned for human uses. The modern view of the archipelago soon emerged a place of scientific wonder and positive enchantment.

Acknowledgments

The author would like to thank Michael Ghiselin, Alan Leviton, and Michele Aldrich for their exceptional editorial assistance with this article and the University of Georgia Libraries for access to and permission to publish illustrations from early published works about the Galápagos Islands.

[27] Ibid., 263.

[28] Ibid., 167.

[29] Ibid., 255, 263. These four escaped goats were the first of many feral animals to flourish on James and other islands, with devastating impact on native species.

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"A Universal Collector": Charles Darwin's Extraction of Meaning from his Galápagos Experience

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It is well known that during the voyage of H.M.S. *Beagle* Charles Darwin collected specimens in geology and botany as well as in zoology. It is also well known that his work in the Galápagos Islands in September and October 1835 represented a turning point in his career. This article examines his collecting practices in natural history while on the Islands, with particular attention paid to his geological observations and collections at James Island (Isla Santiago). It suggests that his search for significance was bound up with his pattern of collecting and that he wrung meaning from even small suites of specimens, whether mockingbirds or igneous rocks.

Whewell introduced me to Mr. Darwin, with whom I had some talk; he seems to be a universal collector.[1]

The theme of the conference held at the California Academy of Sciences on August 14–15, 2009 was concisely expressed by its title: "Darwin and the Galápagos." The focus was singularly appropriate to the sponsoring institution inasmuch as the California Academy has led the way in scientific research on the islands beginning with its 1905–1906 expedition and continuing through the 1964 Galápagos International Scientific Project whose co-director was Robert I. Bowman (James, this volume; Leviton and Aldrich, this volume). The 1964 expedition was notable for including all the areas of science that Charles Darwin himself studied: geology, zoology, botany. (Bowman 1966; Bowman, Berson, Leviton 1983). In addition to shorter reports, systematic treatments of the Galápagos geology and botany stemmed from the 1964 expedition. Of particular interest to me, two geologists from the 1964 expedition — Alexander R. McBirney of the University of Oregon and the late Howel Williams of the University of California, Berkeley — published a monograph describing their field work in 1969 in which they integrated Darwin's findings with their own (McBirney and Williams 1969). In 2007 I was a member of a team of historians and geologists who redid a portion of Darwin's geological research on the islands, building on the foundation that McBirney and Williams had laid (Herbert et al. 2009; Gibson 2009).[2] As with work on the geology, results on the systematic botany were published following the 1964 expedition, stimulating further work of an historical nature (Wiggins and Porter 1971; Porter 1987).

An enduring accomplishment of the 1959 celebrations in honor of Darwin was the establishment of the Galápagos National Park and the Charles Darwin Research Station. Conservation was the order of the day in 1959 on the islands, and the Galápagos were soon to become one of the world's wildlife reserves (Larson 2001; Riley and Riley 2005). In a parallel fashion, the past fifty years have been devoted to conservation and public presentation of the historical record. The record includes not only texts but also specimens. In geology, Darwin's "Notebook A" was pub-

lished in 1987; a transcription of Darwin's geological notes from the Galápagos Islands was recently posted online; and a significant portion of Darwin's geological collections from the voyage are now on display at Sedgwick Museum of Earth Sciences in Cambridge.[3] A fuller textual record, combined with access to specimens, has also allowed researchers to return to the sites Darwin studied with renewed interest and possibility of recreating his work.

Darwin published three books on his geology stemming from the *Beagle* voyage: the first, and most famous, of these works was devoted to coral reefs, the second to volcanic islands, and the third to the geology of South America (Darwin 1842, 1844, 1846). As the most influential of the three, the work on coral reefs has merited the greatest attention, signaled by D.R. Stoddart's edition of Darwin's first version of his theory written during the voyage (Stoddart 1962). The second part of Darwin's trilogy, devoted to volcanic islands, forms the geological thread of my paper here. Darwin's third volume on the geology from the voyage has also sparked interest in the 2009 bicentennial year. An issue of *Revista de la Asociación Geológica Argentina* entitled "Darwin in Argentina" was published in English by South American geologists currently working in the areas Darwin visited.[4] This important work effectively brings Darwin's researches described in the third volume of his trilogy into the present.

In the integrative spirit of the "Darwin and the Galápagos" conference, I would like to pursue a question that arose in connection with my own and my colleagues' inquiries in 2007 into Darwin's geological work on the islands but which has ramifications beyond geology. I will ask how Darwin's geological collecting practices and theorizing on the islands compare with his work in zoology and botany.

Specimens

Let me begin discussion of Darwin's geological findings from *Volcanic Islands* (1844) with consideration of the specimens. The discrepancy between the presence of Darwin's geological specimen 3268 as it existed in a cabinet at the University of Cambridge and the situation on Isla Santiago (James Island) in the Galápagos Islands as Alexander McBirney and Howel Williams found it in 1964 prompted a re-examination of the area in 2007 and 2008 (Herbert et al. 2009; Gibson 2009, and this volume). McBirney and Williams noted that in their own exploration of Isla Santiago they had found no rock corresponding to specimen 3268.[5] In the course of resolving the discrepancy, which involved identifying a site where similar rocks to 3268 were found, we were struck by the relatively small number of geological specimens that Darwin had collected on the island: only 19. In addition, of these 19, a mere 4 specimens figured in his most important inference from his geological study of the island. These four specimens formed the empirical basis for the section of *Volcanic Islands* headed "*On the separation of the constituent minerals of lava, according to their specific gravities.*" (Darwin 1844:117.) Given the paucity of the specimens involved in such a major deduction, an immediate comparison came to mind with the Galápagos mockingbirds: again four specimens were critical.

The question of number of specimens collected by Darwin during the *Beagle* voyage has been raised recently by Melinda Fagan who has compared his collecting practices to those of Alfred Russel Wallace (Fagan 2007). She contrasted their methods on a number of points, a few of which I would like to draw attention to here — the intent behind their collections, the range of their collections, and the number of specimens they collected. While Darwin collected in all areas of natural history, Wallace did not. For example, Wallace did not collect in geology at all. Rather, Wallace focused on those areas of natural history where he could both fulfill his theoretical goal of "solving the problem of the origin of species" and of financing his researches by the sale of duplicate

specimens. According to Fagan, Wallace tailored his collecting activities with regard to what would sell, "concentrating on groups that fetched good prices: tropical birds, butterflies, and beetles" (Fagan 2007:613). On botany, Wallace wrote that "I cannot afford to collect plants. I have to work for a living, and plants would not pay unless I collect nothing else, which I cannot do, being too much interested in zoology" (Fagan 2007:612), Being already committed to an evolutionary perspective when he began to travel as a result of his reading of Robert Chambers's anonymously published *Vestiges of the Natural History of Creation* (1844), Wallace set about to distinguish true species from mere varieties and to collect a "good series" of specimens to represent each species and a complete inventory of species at a given locality. (Fagan 2007:616) Wallace's desire to have at hand good series of specimens, coupled with the commercial requirements of his travel, led him to prodigious efforts at collection. As Fagan put it,

> The extent of Wallace's material collection is staggering: over 125,000 specimens collected in the Malay Archipelago alone. His Amazon totals are much lower: roughly 10,000 specimens, mostly butterflies and beetles. This was not due to inexperience or lack of effort. Most of Wallace's South American collection, along with his journals, drawings and notes, was lost on the return voyage to England, when his ship caught fire and sank ten days into the voyage. Wallace's second expedition was more productive, yielding a stupendous total of 125,660 specimens, over 1000 of which represented entirely new species . . . . Unlike Darwin, he appears to have organized his collection by numbering species as well as keeping track of the number of specimens of each (Fagan 2007:617–618).

From Fagan's comparison of Wallace and Darwin's collecting practices one sees quickly how differently it was possible to organize one's work as a field naturalist.

As is apparent from the letters that flowed around Darwin's initial appointment to the *Beagle* voyage, collections mattered a great deal: George Peacock, in conveying news of the opportunity to J.S. Henslow wrote of "treasures" that a naturalist might bring home with him, and soon after Henslow wrote to Darwin of his qualifications "for collecting, observing, & noting any thing worthy to be noted in Natural History." Before leaving England Darwin would confer with Francis Beaufort, Hydrographer to the Navy, about the eventual disposition of his collections.[6] As Darwin prepared for the voyage, and for the first several years of it, however, he repeatedly expressed concern about his collection practice. It was chiefly to Henslow to whom he applied for advice. Their relationship was an essential one in Darwin's labors during the voyage for Henslow played many roles in the entire project including accepting consignment of specimens as they arrived back in England. And so Darwin put his questions to Henslow: Were the geological specimens large enough? Yes, replied Henslow, they were. Were the collections too scanty? Darwin pressed the point that Henslow should consider how long he was at sea. Henslow encouraged him on — 'tho you were to send home 10 times as much as you do, yet when you arrive you will often think & wish how you might & had have sent home 100 times as much!" but added that "no one can possibly say you have not been active — & that your box is not capital."[7]

What was the size of Darwin's collections? With a few caveats, one can use his specimen catalogues to estimate the size of his collections. One warning is that each number might correspond to more than one item. Insects, seeds, even grains of sand might be packaged as one item. For example, under Darwin's catalog listing "3365.3366 Small insects" for James Island later classification of the contents described insects as various as Coleoptera, Diptera, Hymenoptera, Lepidoptera, and Hemiptera (Smith 1987:94–96). Another caveat is that in the case of plants, Henslow advised Darwin to number only the important specimens. Duncan Porter has suggested that Darwin numbered as few as one tenth the number of plant specimens he collected (Porter, this volume).

Thus, as Porter has pointed out with respect to the James Island material, Darwin numbered only five plant specimens, whereas he in fact he made 85 collections.[8] Darwin does not seem to have followed this procedure in zoology and geology. Rather, as a routine practice he seems to have numbered most if not all of the zoological and geological specimens he collected. It should of course be borne in mind that other members of the *Beagle*'s company collected specimens that sometimes came to Darwin, and, as work goes forward with historical collections, newly identified specimens associated with Darwin surface from time to time.[9] The enumeration that is possible comes from Darwin's own specimen catalogues. As he explained in his *Journal* of the voyage, he kept two distinct series of numbers, one series with "paper numbers" (meaning the specimens to which paper labels could be affixed, namely the specimens stored dry) and the other with "tin labels" for "specimens in spirits" (Darwin 1839:600). Numbers in the "Specimens in Spirits of Wine" catalog go up to 1529. Numbers in the "Specimens not in Spirits" go up to 3921. (Keynes 2000:369, 421.) The sum of these two numbers is 5450.[10]

What attitude on Darwin's part led to this relatively low number? I will concentrate on his approach to geology. Darwin explained himself as follows to Henslow during the first year of the voyage:

> And now for an apologetical prose about my collection.— I am afraid you will say it is very small.—...The box contains a good many geological specimens.—...I have endeavoured to get specimens of every variety of rock. & have written notes upon all.—...[11]

In the letter Darwin also added a complaint about the difficulty of carrying rocks under a tropical sun, but the key point he made as regard to his collection practice was his simple statement that he sought to collect specimens of every variety of rock. Observation thus preceded collection. This would appear to be the primary reason that the collections were rather small in number: he was interested in identifying the significance of an object before collecting it. Darwin's theoretical orientation is well known so what is being stated here is in the nature of a truism, but one that has particular pertinence when one considers his collecting practices. In addition, in regard to the geological specimens, he was committed to identifying the site of collection. This was a standard procedure for geologists, and one which Henslow again pressed on him in a letter of January 1833: "note all that *may* be useful — most of all, the relative positions or rocks giving a little sketch thus. N°.1. (specimen (a)) about 10 feet thick, pretty uniform in character–N°.2 (specim. (b.c)) variable &c &c[.]"[12] (Fig. 1)

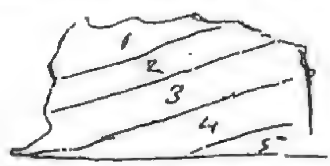

FIGURE 1. Henslow sketch to guide Darwin's geological collecting. (From *The Correspondence of Charles Darwin* 1:292.)

While Darwin only occasionally drew diagrams of the sort Henslow illustrated (see Fig. 2 for one example), he was diligent in recording locations of his specimens to the best of his ability. Since he sometimes carried a mountain barometer, his measurements of height are more easily duplicated today than his compass directions, which are less exact. In any case, given the constraints of time he faced, his collection practice was remarkable as judged, for example, by his work on James Island where he managed to collect a broad range of the available rocks (Gibson, this volume).

When considering Darwin's practices as a collector, there is an additional relevant aspect drawn from recent scholarship on Henslow that connects to Darwin's interest in finding bridging variations or series among specimens and also connects to Wallace's focus on collecting series of specimens. The new work on Henslow done over the course of the last twenty five years has been substantial (Walters and Stow 2001). Of particular relevance to Darwin's practice has been the dis-

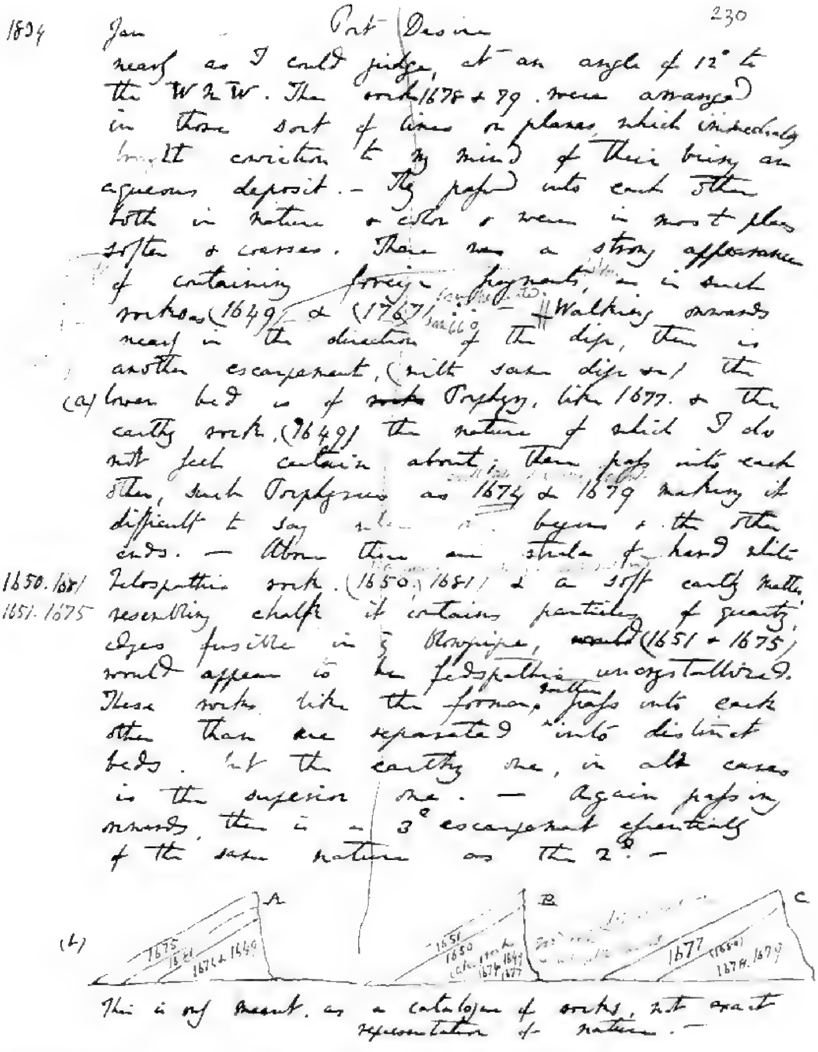
1834 Jan Port Desire 230
nearly as I could judge, at an angle of 12° to
the WNW. The rocks 1678 & 79. were arranged
in those sort of lines or planes, which immediately
brought conviction to my mind of their being an
aqueous deposit. — They passed into each other
both in nature & color & were in most places
softer & coarser. There was a strong appearance
of containing foreign fragments, as in such
rocks as (1649) & (1767) — Walking onwards
nearly in the direction of the dip, there is
another escarpment, (with same dip &c) the
(a) lower bed is of ~~rock~~ Porphyry, like 1677. & the
earthy rock, (1649) the nature of which I do
not feel certain about; these pass into each
other, such Porphyries as 1674 & 1679 making it
difficult to say [illegible] [illegible] begins & the other
ends. — Above these are strata of hard white
1650. 1681 Felspathic rock. (1650, 1681) & a soft earthy matter
1651. 1675 resembling chalk it contains particles of quartz,
edges fusible in [illegible] Blowpipe, ~~would~~ (1651 & 1675)
would appear to be felspathic uncrystallized.
These rocks, like the former, rather pass into each
other than are separated into distinct
beds. but the earthy one, in all cases
is the superior one. — Again passing
onwards, there is a 3rd escarpment essentially
of the same nature as the 2nd. —

FIGURE 2. From DAR 33:230. (Darwin Archive, Cambridge University Library.)

covery that Henslow practiced a method of plant collection — "collation" — that emphasized the importance of variation within species:

> A collated Henslow sheet carries several plants of a single species from one or more locations, each typically numbered directly on the sheet, with a label recording location, date of collection and collector's name. Collated sheets usually carry two or three plants, but there may be as many as 32. Two-thirds of the sheets are collated and 90% of these show variation in height, leaf shape, branching pattern or flower colour. Collated sheets that show height variation have several distinctive display patterns, such as bell curves and ascending/descending series. They can depict continuous variation within a single population, or may include plants from across Britain. (Kohn, Murrell, Parker, and Whitehorn 2005:643)

Since Darwin was enrolled in Henslow's botany lectures all three years he was at Cambridge,

TABLE 1. Darwin's Specimens Collected on James Island (Isla Santiago)[1]

Geological Specimen Notebooks		Specimens not in Spirits		Specimens in Spirits
		3263	Various Cellariae, encrusting Corallines &c from 40 Fathoms deep[3]	1307 Arachniade (sweeping)[2]
				1308 Snake
				1309 Body of bird (3374)[4]
		3264	Gorgonia[5]	1310 Snake
				1311 Salt water from Salina in crater at James Is^{d}
3265	Trachytic cellular Lava [basalt][6]			
3266	Base.blackkish grey [basalt]			
3267	Olivine do [ditto- as 3266] [trachyandesite]			
3268	Compact greenish gray Lava [trachyte]			
3269	Finely & much cellular Trachyte [basalt]			
3270	do [ditto] [leucogabbro]			
3271	[ditto]			
3272	[ditto] [gabbro]			
3273	[ditto]			
3274	do [ditto] [missing specimen]			
3275	Red irregular fracture Claystone base [olivine basalt]			
3276	Volcanic Sandstone			
3277	[ditto]			
3278	Trachyte [basalt]			
3279	Gray. compact do [ditto] [trachyandesite]			
3280	Blackish grey Lava [olivine basalt]			
3281	do [ditto] blacker, more cellular [vesicular olivine basalt]			
3282	Orange brown Sandstone			
3283	do [ditto] Volcanic Sandstone			
		3284	Cactus[7]	
*missing numbers 3290 & 3292				
		3293	Large succulent, climbing plant[9]	
		3294	Syngynesia; the characteristic & <u>abundant</u> tree in the high ground[10]	
		3295	Common tree in the intermediate ground[11]	
		3303	Owl[12]	
		3304	Gull[13]	
		3310	Wren[14]	
		3330	Finch (with parrot beak) M. James Is^{d}	
		3331	do [ditto] F.[15]	
		3350	Thenca[16]	
		3360	Rat James Is^{d}.[17]	
		3365:66	Small insects James Is^{d}[18]	
		3368:69	Lands [*sic*] shells. James Id.	
		3370	Sea shells. tidal rocks do [ditto]	
		3374	Anthus James Is^{d}.[19]	

[1] Unless otherwise noted specimens listed were associated by Darwin with James Island in particular rather than with the Galápagos Archipelago in general. Identifications have been abbreviated.

[2] Keynes 2000, p. 362 has "<u>James Is^{d}</u>." listed above the entry.

[3] Keynes 2000, p. 413: Busk Collection: *Mucronella ventricosa*. Specimens 3263 and 3264 were corals collected underwater. Since they immediately precede 3265, a specimen known to have been collected on James Island, I take them to have been collected *en route* to or in the vicinity of the island.

[4] Keynes 2000, p. 417: 3374 is labelled by Darwin "Anthus James Is^{d}. listed as *Dolichonyx oryzivorus* in *Zoology* 3:106 and labelled 3374D at the Natural History Museum (London).

[5] Keynes 2000, p. 290-291: Gorgonacea, horny octocorals.

it is fair to assume that he was introduced to Henslow's ideas there. The University Herbarium at Cambridge owns 950 sheets containing about 2,600 plants collected by Darwin during the *Beagle* voyage.[13] John Parker has identified one sheet of a grass (*Vulvia*) from Darwin's *Beagle* collection where Henslow had arranged four specimens to illustrate "extreme size variation" of the plant.[14] In writing to Darwin while he was on the voyage, Henslow's advice was simpler: "Most of the plants are very desirable to *me*. Avoid sending *scraps*. Make the specimens as perfect as you can, *root, flowers & leaves* & you can't do wrong . . . . and a single label *per month* to those of the same place is enough except you have plenty of spare time or spare hands to write more."[15] Darwin did indeed bring such botanical specimens home as Henslow desired, and something of the criteria for recognizing variation can be presumed to have affected his overall collecting practice.

On sheer number, then, Darwin's collecting method on James Island seems consistent with his practice on the voyage in its entirety: collect specimens of significance. The next point to be noted is the broad range across which Darwin collected: geological, botanical, and zoological. The distributional pattern illustrates his varied interests (Table 1). The sequentially numbered geological specimens illustrate his activity in the early portion of the stay on the island. Trachytes, basalts, and volcanic sandstones are listed. The botanical listings are many fewer, though, as mentioned above, they represent only a small portion of what he collected. Still, a genus unique to the Galápagos — the *Scalesia* or (to use a present-day expression) "daisy trees" — are represented (Fig. 3). The zoological specimens include a mockingbird (specimen 3350) — referred to as its Chilean indigenous name of "Thenca" (Darwin, ed., 1841, *Zoology* 3:61). While, as is well known, Darwin did not systematically note the island of origin of the Galápagos finches, he did so for specimen 3330. Overall, despite the relatively small number of specimens Darwin collected at James Island, it is impressive how much meaning he extracted from them. For that meaning we must consult his written evaluations.

From contemporary texts it is clear that the theoretical issue at the forefront of Darwin's mind in 1835 was the origin and distribution of coral reefs. Before leaving the coast of South America

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6 In this column the brief characterizations of the rock specimens are from Darwin's geological specimen notebook (DAR 236), also available in fair copy as the Harker Catalogue. The present-day identifications listed in brackets were done by Dr. Sally Gibson at the University of Cambridge and are taken from Table 1 of Herbert et al. 2009, pp. 9-11. See that publication for fuller information.

7 Keynes 2000, p. 413: *Opuntia galapageia* from Porter 1987, pp. 183-184. Darwin noted the specimen as from James Island. J.S. Henslow described the cactus (Henslow 1837).

8 Keynes 2000, p. 413; Porter 1987, p. 184.

9 Keynes 2000, p. 413; Porter 1987, p. 184: *Peperomia galioides*.

10 Keynes 2000, p. 413; Porter 1987, p. 184: *Scalesia pedunculata*.

11 Keynes 2000, p. 413. In the full entry Darwin wrote that "All the above 5 species of plants come from James Is^{d} [3284, 3285, 3293, 3294, 3295]." Specimen 3295 is *Psidium galpagageium* (Porter 1987, p. 185).

12 Keynes 2000, p. 414; *Zoology* 3:32-33 where the habitat for the owl is listed as James Island.

13 Keynes 2000, p. 414; *Zoology* 3:141-142: *Larus fuliginosus*.

14 Keynes 2000, p. 414; *Zoology* 3:106: *Certhidea olivacea* where Darwin commented "I believe my specimens...were procured from Chatham and James Islands; it is certainly found at the latter."

15 Keynes 2000, p. 414; *Zoology* 3:103 *Camarhynchus psittaculus* for specimens 3330 and 3331.

16 Keynes 2000, p. 416; *Zoology* 3:62: *Mimus melanotis*.

17 Keynes 2000, p. 416; *Zoology* 2:34-35: *Mus Jacobiae*.

18 Keynes 2000, p. 416; Smith 1987:94-95 lists scientific names for the numerous insects.

19 Keynes 2000, p. 417; *Zoology* 3: 106: *Dolichonyx oryzivorus*. Darwin remarked that "This bird was shot by Fuller on James Is^{d}" (Keynes, p. 298). The bird is also listed under "Specimens in Spirits" number 3109.

he had written down his key insight respecting "a Corall bed, forming as land sunk." At the Galápagos he speculated over the lack of reefs, paying great attention to Captain Robert FitzRoy's suggestion that the water was too cold for abundant production of corals, though even near James Island he did collect coral specimens 3263 and 3264. As it turned out, the Galápagos was a mere way station for his coral reef theory, for at his very next stop in Tahiti he had the illuminating experience of gazing down at the small coral island of Ei Meo (Moorea) from the heights of the main island and imagining how a "Lagoon Is^{d}." (atoll) would be formed should the ocean floor subside. From these insights, by the end of 1835 he was able to write a formal essay, entitled "Coral Islands," describing his theory of the formation of coral reefs through subsidence (Stoddart 1962; Herbert 2005:168–171). When the *Beagle* reached the Keeling Islands in April 1836, Darwin was able to make an extensive on-site examination of reefs with his theoretical insights to guide him.

FIGURE 3. Scalesia pedunculata, *Hook. fil.* Herbarium sheet from Charles Darwin's *Beagle* collection. (By permission of the Cambridge University Herbarium.)

By comparison his deepest insights into the zoology and botany of the islands were promising but not yet well developed. The same can be said for his insights into processes he would eventually describe under the heading of the "separation" of lavas (Darwin 1844:117). Before examining parallels between theorizing further, let us put on record his report on his Galápagos experience as he described it in a letter to Henslow written from Sydney in January 1836:

> I last wrote to you from Lima, since which time I have done disgracefully little in Nat:History; or rather I should say since the Galapagos islands, where I worked hard.— Amongst other things, I collected every plant, which I could see in flower, & as it was the flowering season I hope my collection may be of some interest to you.— I shall be very curious to know whether the Flora belongs to America, or is peculiar. I paid also much attention to the Birds, which I suspect are very curious. The Geology to me personally was very instructive & amusing; Craters of all sizes & forms, were studded about in every direction; some were such tiny ones, that they might be called quite Specimen Craters.— There were however a few facts of interest, with respect of layers of Mud or Volcanic Sandstone, which must have flowed liked [sic] streams of Lava. Likewise respecting some grand fields of Trachytic Lava.— The Trachyte contained large Crystals of glassy fractured Feldspar & the streams were naked bare & the surface rough, as if they had flowed a week before.— I was glad to examine a kind of Lava, which I believe in recent days has not in Europe been erupted.— [16]

If one compares his account here to the chapter he devoted to the Galápagos in his published account of the voyage, most of the elements are there — the peculiar birds and plants, the volcanic

sandstones (Darwin 1839:453–478). What is missing in the published version but what obviously interested him in January 1836 was the question of types and dates of lava and some discussion of crystals in lava. This subject would not be treated until publication of *Volcanic Islands* in 1844.

While the subject of the importance of Darwin's work on James Island for the understanding of igneous processes has been discussed elsewhere, I will begin by outlining his idea in brief (Harker 1909; Pearson 1996; Herbert 2005:120–126; Herbert et al. 2009; Gibson 2009 and this volume). In 1835 as Darwin came to Galápagos he was working with a basic distinction for categorizing eruptive rocks into two series, the trachytic and the basaltic, based largely on silica content. Trachytes contain relatively more silica than basalts and hence are generally lighter in color. The interpretive significance of this distinction was then a matter of discussion (Oldroyd 1996:192–203; Young 2003:125–140). Darwin's observations on James Island were relevant to this discussion, for he showed that trachytes and basalts could exist in close proximity to each other and grade into one another. This was the significance of specimens 3265, 3266, 3267, and 3268. His observations were the basis of his published work (Darwin 1844:117–118). Thus, it was of interest when McBirney and Williams reported finding no specimen like 3268 (the trachyte) on the island.[17] In subsequent laboratory work on Darwin's geological specimens from the island, which involved close comparison with collections made with Darwin's manuscripts, Sally Gibson was also able to show that he had to revise a number of his initial identifications of the rocks once he returned to England. (Herbert et al. 2009; Gibson 2009 and this volume). However, the designation of specimen 3268 as a trachyte stayed firm.

Darwin titled Chapter 6 of *Volcanic Islands* "Trachyte and Basalt — Distribution of Volcanic Islands." It was the only chapter in the book that had a theoretical title. In it he argued for the "separation of constituent minerals of lava, according to their specific gravities." He then went on to the even more interesting idea that eruptive rocks separated into the trachyte-basalt series as they cooled by a process of crystallization of some of the constituent materials of the lava. He suggested, "The sinking of crystals through a viscid substance like molten rock . . . is worthy of further consideration, as throwing light on the separation of the trachytic and basaltic series of lavas . . . . In a body of liquefied volcanic rock . . . we might expect . . . that if one of the constituent minerals became aggregated into crystals or granules , . . .such crystals or granules would rise or sink, according to their specific gravity" (Darwin 1844:118–120). By the mid-1840s, Darwin was increasingly involved with work on transmutation that he did not pursue these ideas in later publications, and without his advocacy they received little immediate attention. Later Alfred Harker at the University of Cambridge, in his book *The Natural History of Igneous Rocks*, would evoke evolutionary ideas (not "special creations") to describe the process of magmatic differentiation:

> That the actual diversity met with among igneous rocks and the varying composition of many single rock-bodies are in the main attributable to processes of differentiation is a thesis which needs no formal discussion. It has been the common ground of almost all speculations on this subject during the last sixty years — that is, since the date of Darwin's Geological observations on the volcanic Islands. . . . The only practical alternative to magmatic differentiation, as accounting for the observed facts, is the doctrine of countless special creations (Harker 1909:310).

Harker also credited Darwin's understanding of the role of crystallization as derived from his experiences at James Island. Harker noted that "even when crystallization proceeds uniformly throughout a body of rock-magma, important consequences may result from a partial mechanical separation between the crystals already formed at a given stage and the residual fluid magma"(Harker 1909:320). He suggested that:

> One process which readily suggests itself is the *sinking of crystals* in a fluid magma. this was long ago maintained by Darwin as a principal cause of differentiation. After noticing instances of lavas in which porphyritic crystals have accumulated at the bottom, he remarked that such facts "throw light on the separation of the trachytic [i.e. acid] and basaltic series of lavas." He clearly connected it with progressive crystallization in the magma. On the one hand, he considered that a separation due to gravity could not be effective, as had been supposed by [George Poulett] Scrope, in a magma still wholly liquid; on the other hand, there would be no sinking of crystals if all the minerals crystallized simultaneously, which he believed to be the case in plutonic rocks (Harker 1909:321).[18]

Harker also credited Darwin for accounting for an initial eruption of trachyte in cases where both trachytic and basaltic streams have proceeded from the same orifice, noting that the molten lava of the trachytic series had accumulated in the upper parts of the volcanic focus.

Nineteen years after Harker wrote *The Natural History of Igneous Rocks* another important book in the field appeared that, again, drew a rhetorical analogy between biological and mineral diversification. This was Norman Bowen's *The Evolution of the Igneous Rocks* (Bowen 1928). Bowen did not mention Darwin by name — his historical references do not go that far back into the nineteenth century — but the title he chose for his book made the connection. In his preface Bowen made the qualifying remark: "The use of the term 'evolution' in the title is intended to designate only a process of derivation of rocks from a common source and not to imply that detailed knowledge of the process which the term connotes when applied to organic development (Bowen 1928:v). Still, when Bowen gave one of his chapters the title "The Liquid Lines of Descent and Variation Diagrams" one senses his affinity with the notion of evolutionary phylogenies (Bowen 1928:92). In addition to the notion of common descent, Bowen's work showed continuities with the particulars of Darwin's work on igneous rocks. Bowen's specialty was the investigation of crystallization processes of rock formation studied in a laboratory setting. Thus, he shared Darwin's much earlier interest in crystallization. Based on his experimental studies Bowen noted that "We find in a certain investigated system a definite course of crystallization and definite possibilities of differentiation through fractional crystallization" (Bowen 1928:63). Darwin's brief excursion into petrological theory drawn from work on James Island was congruent to ideas that Bowen would develop much later and in a laboratory setting (Pearson 1996). The vocabulary the two men employed overlapped. Darwin wrote of "separation"; Bowen wrote of "differentiation." Bowen used the word "fractional"; Darwin did not. Both men wrote of "crystals" and of "crystallizaton" or (in British spelling) "crystallisation."

Common Thread

Let us now return to October 1835 and Darwin's experience. Our central question is whether there was a common thread running through his work. Clearly he was economical with respect to numbers in his attitude to collecting. But was there a common philosophical orientation in his Galápagos work? At the very broadest level there was. While entertaining alternative points of view, Darwin favored an approach that identified currently observable processes. As has been established by numerous authors, this approach was associated with Darwin's growing regard for Charles Lyell's *Principles of Geology* (1830–1833). While working on igneous rocks on James Island, Darwin drew most on Lyell's close associate George Poulett Scrope, who had preceded Lyell in emphasizing the geological role of presently active causes and an Earth of great though unspecified age. In a sense Scrope was Lyell's surrogate regarding interpretation of the volcanic rocks on

Isla Santiago.[19] Lyell's interests, like Darwin's, were broader than Scrope's, however, and, as is well known, Darwin made full use of Lyell's emphasis on "centres of creation" in treating zoological and botanical questions.

Overall Darwin's most significant finding from his Galápagos experience derived from the four specimens of mockingbirds he collected: 3348, 3359, 3306, and 3307 (Keynes 2000:298; Herbert 1980:66, 116–117). Like the four trachyte/basalt specimens from James Island, the four mockingbirds posed a problem of explaining diversity. Darwin was pleased to note immediately that the mockingbirds were like those he had seen on the South America continent. This was to be expected on Lyellian terms. He also asked in his field notebook "I certainly recognise S. America in ornithology, would a botanist?" (Chancellor and Van Wyhe 2009:439.) There was another pattern of distribution with the mockingbirds, quite unexpected by him, that would turn him to embrace transmutation. In his first stop at the Galápagos, on Chatham Island (San Cristobal), he saw mockingbirds; on his second stop, on Charles Island (Floreana), he saw a noticeably distinct mockingbird, one with dark feathers on its chest (Fig. 4). Why were the mockingbirds of islands so close to each other distinct? From this unexpected dissonance emerged an attention to the mockingbirds on the other islands he visited.[20]

It is generally acknowledged by historians of science that Darwin's insight into the unexpected distribution of the mockingbirds represented the single most important turning point on his road to becoming an evolutionist. It is therefore worth noting the similarities and differences between the mockingbird case and that of the James Island (Santiago) trachyte and basalt collection. Both cases involved consideration of the islands in relation to the South American continent. In both cases Darwin was self-confident in his ability to recognize and collect novelty. As to differences, the kinds of distributional patterns that were appropriate to species ("centres of creation") did not

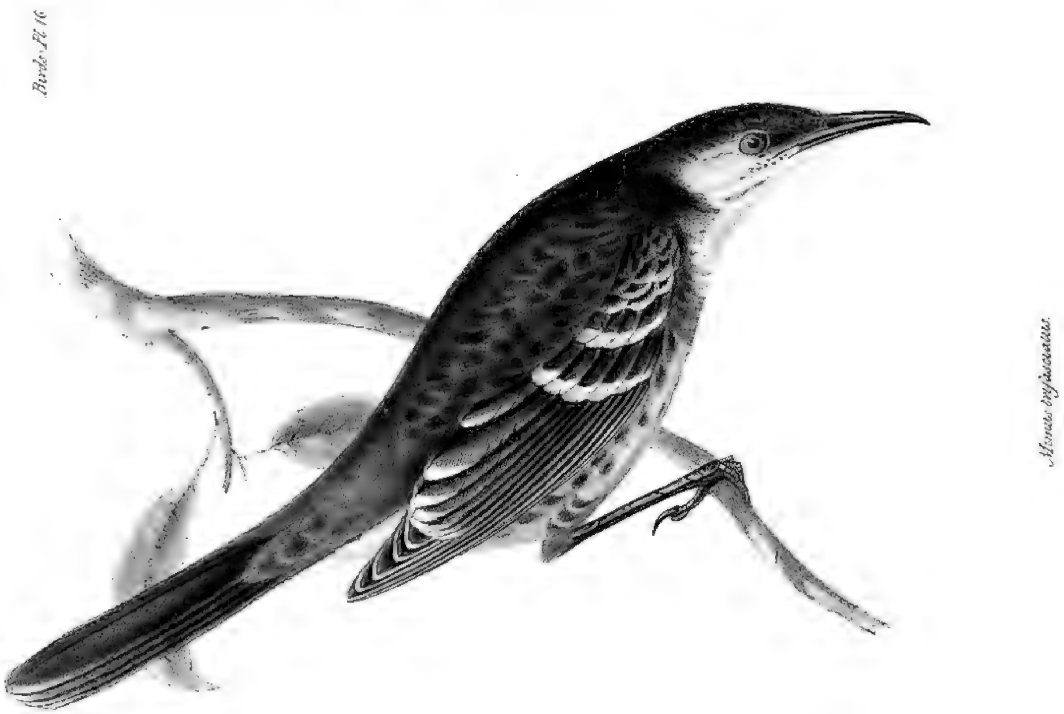

FIGURE 4 Charles Island (Isla Floreana) Mockingbird (*Mimus trifasciatus*, now *Nesomimus trifasciatus*). (Illustration from Darwin 1841, *Birds* by John Gould, pl. 16.)

apply directly to rocks. There was a presumption among geologists that rock types were universal, though questions of geographical distribution remained.[21] Initially, based on examination of Darwin's four rock specimens, I had hypothesized that the site of collection might have been missed by McBirney and Williams owing to subtlety of difference comparable to that in the mockingbirds (Herbert 2005:123). However, the larger field specimens showed a more dramatic difference in overall physical appearance than Darwin's original and much smaller hand specimens.[22] (Fig. 5)

FIGURE 5 Four rock samples photographed on porch at Cactus Pad (Isla Santa Cruz). The trachyte believed to be from the site where Darwin collected specimen 3268 is on the lower left. (Photo by Sandra Herbert, July 2007).

A final difference between the circumstances surrounding the mockingbirds and the James Island rock collections was regard to timing. Darwin's contemporary notes on the Galápagos mockingbirds reflect a more advanced development of his ideas on the subject than do his contemporary notes on the James Island rocks. This difference in stage of development of ideas would widen in the succeeding months of the voyage, with Darwin's work on species and on other subjects, especially coral reefs, advancing rapidly, while work on the genesis of rock type diversity is present but occupies comparatively less space in his notes. Darwin wrote his essay entitled "Coral Islands" in late 1835 shortly after visiting Tahiti (Stoddart 1962). Later in the process of making separate lists of specimens for specialists in different areas, Darwin made the first unmistakable commitment to exploring the subject of transmutation in his comment on the island-by-island distribution of the mockingbirds (". . . such facts would undermine the stability of Species" [Barlow 1963:262]). During the last year of the voyage Darwin also continued to ponder the subject of the genesis of rocks but, insofar as I have been able to ascertain, without focusing on the James Island site of specimens 3265 through 3268. As examples of his ongoing interest in what he termed "Volcanic theory" here are some passages written in the closing months of the voyage:

> Volcanos must be considered as chemical retorts.— neglecting the first production of Trachyte. look at Sulphur. salt. lime, are spread over [added: whole] surface; how comes it they do not flow out together? How are they eliminated.— [added: Sulphur last.—] Metallic veins likewise must separate ingredients if we look to a constant revolution.—

and

> Volcanos blend all substances together; & products being similar over whole world. general circulation (Herbert 1980:52, 60).

In sum, Darwin was keenly interested in the processes involved in a "constant revolution" of materials within volcanoes, but his quite general speculations were not attached to the particular site in the Galápagos that would figure so prominently later in *Volcanic Islands* (1844).

On his return to England in October 1836, Darwin entered one of the busiest and most complex periods in his life. He was seeking expert assistance from numerous individuals in describing and interpreting his specimens. He also felt the pressure of time, for he wanted his portion of the narrative of the voyage to include reports on key specimens, including those from the Galápagos, to which he devoted an entire chapter (Darwin 1839, Chapter 19). To take but one example, John Gould described three of the Galápagos mockingbirds as separate species at a meeting of the Zoological Society of London on February 28, 1837.[23] The new material on Galápagos ornithology quickly found its way into Darwin's account of the voyage (Darwin 1839:461–462). In botany Henslow was able to do some work on the Galápagos specimens, but the major portion of the work was left to Joseph Hooker in the 1840s (Henslow 1837; Darwin 1839:460; Hooker 1847a, 1847b). The result of this was that it was only in the second edition of Darwin's narrative from the voyage that the Galápagos botany appears to full effect, complete with a table (Fig. 6) indicating the total number of endemic species found on each of the four islands on which Darwin collected. The endemic Galápagos "daisy tree" or *Scalesia* received full attention: "Scalesia, a remarkable arborescent genus of the Compositae, is confined to the archipelago: it has six species; one from Chatham, one from Albemarle, one from Charles Island, two from James Island, and the sixth from one of the three latter islands, but it is not known from which: not one of these six species grows on any two islands" (Darwin 1845:396). On the zoological side Darwin's second edition of his voyage account included information on the adaptive significance of the Galápagos finches (Darwin 1845:379–380). On the geological aspect, Darwin's lava specimens from James Island (3265 through 3268) play no explicit role at all in either edition of the voyage account. However, in the second edition Darwin did characterize the Galápagos Islands as "formed of basaltic lava" and therefore different "in geological character from the American continent" (Darwin 1845:393). Darwin's ultimate judgment concerning the predominantly basaltic nature of Galápagos lavas has been sustained over time (Simkin 1984).

396 GALAPAGOS ARCHIPELAGO. [CHAP. XVII.

Name of Island.	Total No. of Species.	No. of Species found in other parts of the world.	No. of Species confined to the Galapagos Archipelago	No. confined to the one Island.	No. of Species confined to the Galapagos Archipelago, but found on more than the one Island.
James Island .	71	33	38	30	8
Albemarle Island	46	18	26	22	4
Chatham Island.	32	16	16	12	4
Charles Island .	68	39 (or 29, if the probably imported plants be subtracted)	29	21	8

FIGURE 6. Table of information Darwin obtained fromJoseph Dalton Hooker and included in the second edition of Darwin's *Researches* (1845:396) indicating the total number of endemic species found on each of the four islands on which he collected.

In comparison with other features of his Galapagos experience, Darwin's ideas on lava separation appear only in 1844. There was thus a considerable delay between the time of his collections of specimens and his initial observations to development of his ideas and their publication.[24] By

way of contrast, his first publication of his theoretical explanation for the origin and distribution of coral reefs was at a meeting of the Geological Society of London on May 31, 1837 (Darwin 1837). Darwin had arrived home with a written exposition of his coral reef theory; he also had the advantage of a sponsor for his views — Charles Lyell — who actively promoted them at the Geological Society (Stoddart 1962; Herbert 2005:232–244).

During the 1835–1844 interval Darwin's full views on trachyte and basalt separation were not worked out in any surviving manuscript known to me. It should also be noted that during the interval the man on whose work Darwin had drawn the most — George Poulett Scrope — had set aside his geological career for one in politics. There was no one to serve as the insider figure at the Geological Society to foster discussion of role of crystallization in the formation of different series of igneous rocks. (Darwin's Cambridge advisor on minerals, William Hallowes Miller, did not play that role.) In this respect, Scrope's career trajectory was somewhat like that of Henslow. The professions of both men were changing — Scrope's for politics, Henslow's for the church — just at the time when Darwin was looking for strong scientific alliances. In the case of botany Joseph Hooker would eventually serve as Darwin's scientific collaborator. In the case of the trachyte-basalt issue, Darwin would publish on his own. In time Scrope would re-interest himself in geology and draw attention to Darwin's expansion and affirmation of his own work on crystallization. However, that would not happen until the mid-1850s.

While Darwin did not leave behind an early statement of his theory of trachyte-basalt separation, we do know that he had completed what was presumably the descriptive chapter on Galápagos geology by January 1838 (Burkhardt et al. 2:431). We also know from his entries in Notebook A, the post-voyage notebook assigned to geology, that he continued to speculate and read on a variety of topics, including the nature and difference among rock types (Barrett et al. 1987). Perhaps most interesting, however, are clues contained within his published work that suggest the development of his thinking. As Paul Pearson suggested some years ago, there is an analogy between Darwin's idea of natural selection and his idea of the separation of lava types. To quote Pearson:

> Most fundamentally . . . the specific mechanisms that Darwin suggested for magmatic differentiation and organic evolution have striking similarities. The former theory . . . is that the crystallization and removal of a mineral from a body of molten rock inevitably causes a chemical change in the remaining melt . . . Subtraction is also the essence of natural selection. Thus, if a particular animal displays a disadvantageous trait, it is likely to be removed, by death, from the population (Pearson 1996:64).

With regard to Pearson's thesis, it is interesting to note that the author from whom Darwin took the most in understanding the process of separation was H.L. Pattinson who published his ideas at about the same time as Darwin was reading Thomas Robert Malthus (Herbert 1971). Pattinson presented a paper entitled "On a New Process for the Extraction of Silver from Lead" at the Newcastle meeting of the British Association for the Advancement of Science in August 1838 (Pattinson 1839). Darwin did not attend the Newcastle meeting, though he followed its proceedings. Darwin described Pattinson's discovery as follows:

> A valuable, practical discovery, illustrating the effect of the granulation of one element in a fluid mass, in aiding its separation, has lately been made; when lead containing a small proportion of silver, is constantly stirred whilst cooling, it becomes granulated, and the grains or imperfect crystals of nearly pure lead, sink, to the bottom, leaving a residue of molten metal much richer in silver; whereas if the mixture be left undisturbed, although kept fluid for a length of time, the two metals show no signs of separating....In a body of liquefied volcanic rock, left for some time without any violent disturbance, we might expect, in accordance with the above facts, that if one of the constituent minerals became

> aggregated into crystals or granules, or had been enveloped in this state from some previously existing mass, such crystals or granules would rise or sink, according to their specific gravity.[25]

As Pearson correctly pointed out, both natural selection and the Pattinson sequence are subtractive processes, and it is indeed interesting that Darwin could have been entertaining both notions in September 1838. I know of no textual evidence that ties Darwin's reading of Thomas Robert Malthus at the end of September 1838 to his learning of Pattinson's work on lead-silver separation, but the possibility of overlapping lines of influence.

Promotion of Darwin's Ideas on Volcanoes

Whatever the process of discovery, Darwin did publish his explanation of "the separation of the constituent minerals of lava, according to their specific gravities" in 1844. Does it then make sense to credit Harker's claim that the notion of "differentiation" has been the "common ground" of "almost all speculations on this subject during the last sixty years – that is, since the date of Darwin's *Geological Observations on the Volcanic Islands*"? While there is a grain of truth in Harker's remark, the notion that Darwin provided the "common ground" on which other authors built is an exaggeration.

As Darwin himself commented to Lyell in 1843 while writing the *Volcanic Islands* manuscript, "I hope you will read my volume for if you don't I can't think of anyone else who will!—" (Burkhardt et al. 2:338). Darwin was aware that interest in the Geological Society in igneous rock formation was low, and that, owing to chronic illness, he was unable to promote his ideas in person. It was not until later in the nineteenth century that petrology became of general interest, consequent partly on the development of chemistry as an allied field, and partly on the development of such techniques as microscopical examination of rocks in thin section. However, Darwin's *Volcanic Islands* did find readers. Charles Daubeny did not adopt Darwin's views on lava separation, but he cited him on many other points (as coral reef theory) in the second edition of *A Description of Active and Extinct Volcanos* (Daubeny 1848:415–432). Darwin also had other readers, particularly in the United States. In *Mind over Magma* (2003), Davis Young discussed several eminent authors for whom Darwin's *Volcanic Islands* was an important work. These included such prominent geologists as James Dwight Dana, Clarence King, Ferdinand von Richthofen, and Joseph Iddings.[26] What I shall say is supplemental to Young's treatment. What particularly interested me was the question of timing: when did Darwin's comments on lava separation enter the mainstream of British geological thought? To answer this question, I surveyed issues of the *Quarterly Journal of the Geological Society of London* published after 1844.

Interestingly, it was George Poulett Scrope who reawakened interest in Darwin's views. With Lyell's encouragement Scrope had re-entered geology. In 1856 he published an article celebrating the "final extinction of that German romance": "the Wernerian theory of the precipitation from some aqueous menstruum, not merely of granite, and what were then called the primitive formations, but even of all the trap-rocks" (Scrope 1856:327). In the article he did not mention Darwin's ideas of the separation of lavas, but he did mention his ideas on the origin of slaty cleavage (Scrope 1856, p. 347). Then six years later, in 1862, in a second edition of his work on volcanoes — this time dedicated to Lyell — Scrope singled out Darwin for praise on the pertinent point:

> Mr. Darwin concurs with me in the opinion that the lighter felspar-crystals in a mass of liquefied lava will tend to rise to the upper parts, and the crystals or granules of the heavier minerals to sink to the lower; the viscidity of the matter preventing, however, any complete separation of elements differing but slightly in specific gravity (Scrope 1862:125).

All along in his book Scrope distinguished his own views (and Darwin's and Lyell's by association) from the view of such continental geologists as François Sulpice Beudant, who held that trachytes were of "parallel age to the secondary strata and universally prior to the tertiary" (Scrope 1862:128). For Scope, who spent much of his life in Parliament, sorting out views in a partisan fashion came naturally. While Scrope was not apologetic about stating his views firmly, he did not aim for homogeneity in opinion. His anonymous review of the third edition of Lyell's *Principles of Geology* was written in the spirit of a friend who differs sharply on some points.[27] In 1867, his communality with fellow geologists fully restored, Scrope received the Wollaston Medal, the highest award given by the Geological Society of London. Darwin had received the honor in 1859, Lyell in 1866.

By the time Scrope published his second edition of *Volcanos*, Darwin's fame as the author of the *Origin of Species* was well established (Scrope 1862; Darwin 1859). In the Geological Society fellows were eager to bask in the success of their colleague. With his customary rhetorical flair and expansive spirit T.H. Huxley announced in his presidential address of 1869 that geology was governed by "three schools of geological speculation" — "Castastrophism, Uniformitarianism, and Evolutionism" — with the last "destined to swallow up the other two." To Huxley "Evolution . . . embraces all that is sound in both Catstrophism and Uniformitarianism" and "applies the same method to the living and the not-living world, and embraces in one stupendous analogy the growth of a solar system from molecular chaos, the shaping of the earth from the nebulous cubhood of its youth, through innumerable changes and immeasurable ages, to its present form, and the development of a living being from the shapeless mass of protoplasm we term a germ" (Huxley 1869:xlvi-xlvii). Still, two years earlier in his anniversary address of 1867, Warington W. Smyth had discussed crystalline rocks without mentioning Darwin (Smyth 1867). Darwin's *Volcanic Islands* did not yet have touchstone status.

After Darwin's death in 1882, references to his early work in *Volcanic Islands* began to multiply. Moreover, there were interesting tendencies to draw on the language of evolution to describe the origin of rocks as well as to describe the development of such ideas. In 1885, the petrologist T.G. Bonney raised the possibility that "'evolution' may exist among the inorganic products of the earth" (Bonney 1885:75). In 1887, John Wesley Judd (a Darwin confidant) spoke of the "rapidity of evolutions" in geological ideas (Judd 1887:54). In 1888, Judd ended his presidential address by linking his own "honouring friendships of three such men as Scrope, Lyell, and Darwin" (Judd 1888:84). In an 1889 paper, Judd connected Scrope and Darwin as founding figures in the study of igneous rocks (Judd 1889:185–186). In 1890, Judd also contributed fine introduction to the reprints of Darwin's three geological works from the voyage, though without singling out Darwin's work on James Island trachyte-basalt question for mention (Darwin 1890).

The highpoint of treatment of Darwin's role in petrology within the Geological Society came in the presidential address by J.J.H. Teall on February 15, 1901. Teall entitled his address "The Evolution of Petrological Ideas." Under the heading of "The Origin of Species" (meaning rock species in this context) Teal wrote:

> The germs of all the theories which are now struggling for existence can be discovered in the writings of our predecessors. Scrope (1825) held the view that lavas were formed from previously crystallized rocks, such as granite, and maintained that in the process of eruption, or intumescence as he termed it, a kind of differentiation might take place, giving rise to trachyte and basalt. Darwin (1844), in his important work on Volcanic Islands, also discussed the origin of petrographical species. He directed attention to two causes of differentiation which may ultimately prove to be of great importance — (1) the movement of crystals in a magma under the influence of gravity; and (2) the squeezing or leaching-

> out of the more fusible constituents from a partially consolidated or partially fused mass. The first of these he illustrated by the well-known Pattinson process for desilverizing lead, and the second might be illustrated by another metallurgical process often known as liquation . . . by means of which silver is separated from blister-copper (Teall 1901:lxxviii).

Clearly it is not a far step from Teall's remarks to Harker's remarks of 1909, with the qualification that history has been elided and that Scrope's name has been omitted by Harker. Noteworthy is both Darwin's presence in at least some tellings of the story, and, equally important, the adoption of the rhetoric of evolution to tell the story. Bowen's title — *The Evolution of the Igneous Rocks* — had precedents.

CONCLUSION

As indicated by the epigraph to this article, in March 1837 Charles Bunbury, an expert in fossil plants, described Charles Darwin, recently returned from the *Beagle* voyage, as someone who "seems to be a universal collector." This description was apt. In hindsight we may also say that Darwin was an intentional collector. He searched for significance before he collected or (in the case of botany) before he numbered specimens. In sheer number of items, his collections were not large, certainly as compared to those of Alfred Russel Wallace. While there is evidence that he was aware in a general way of variation within any class of natural historical objects, Darwin did not embrace a statistical notion of sampling. Nor, for reasons of practicality as well as imagination, could Darwin hope to keep track of all individuals of any one group as has been done so thoroughly by Peter R. Grant and Rosemary Grant (Grant P. and R. Grant, this volume). Rather, guided by prior training from John Stevens Henslow and others, inspired by his extensive reading during the voyage, and relying on his own very considerable powers of observation and reflection, he collected most of his individual specimens for reasons that made sense within the context of his overarching inquiries.

This is clearly true for Darwin's work on the Galápagos Islands. In zoology the significance of his observations and collections has long been known, though the critical role of the mockingbirds could be understood fully only following publication of Darwin's manuscripts from the voyage. In botany the significance of Darwin's collections on the Galápagos is now clearly understood from the work of present-day botanists. In geology, partly from Darwin's own gliding over of his James Island work in his *Beagle* narrative, the ties of his original speculation to actual specimens have been appreciated only more recently.

As to Darwin's extraction of meaning from his collections, this came over time, at points suddenly (Gould on mockingbirds for example), but yet the process of extraction, from another point of view, went on over the course of a lifetime (Darwin was still weighing the mockingbird case in the 1850s). On plants, his keenest correspondence on the species question in the 1840s through the 1860s would be with Joseph Hooker, the botanist who worked up most of his Galápagos plants, and with Asa Gray, another botanist. In geology, Darwin published his insights on a possible process for explaining the separation of trachytes from basalts in 1844. He was working within a tradition of interpretation that included Lyell and Scrope. That insight was left for others to absorb and pursue. So the process of discovery and communication was uneven. Later petrologists, if they mentioned Darwin at all in connection with the notion of magmatic differentiation, did not customarily cite the Galápagos site and suite of specimens that had taken Darwin's interest. Rock specimens 3265 through 3268 do not have the cachet of the four mockingbirds. Still, from the point of view of recreating Darwin's experience on the Galápagos, we need to take all the elements of his work into consideration. We need to acknowledge that he was indeed a universal collector whose insights spanned all three fields within the domain of natural history: geology, zoology, and botany.

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NOTES

[1] Charles Bunbury to Edward Bunbury, 13 March 1837 (Lyell, K. 1906:95). The conversation took place on March 8, 1837 at a meeting of the Geological Society of London.

[2] As the historian in our 2007 group that re-investigated Darwin's work on Isla Santiago (James Island), I should say in advance that I am deeply indebted to my geologist colleagues — David Norman, Sally Gibson, Dennis Geist — as well as to our expert field guide Gregory Estes and to our photographer Andrew Thurman. The geologists and Greg Estes went onto Isla Santiago to do the field work; Thalia Grant, my husband James Herbert, and I remained behind at Isla Santa Cruz where we coordinated the expedition with the Charles Darwin Research Station and the Parque Nacional Galápagos. In addition to our joint publication, several members of our team have made individual contributions to exploration of the subject and the territory, as indicated in the reference list (Norman 2009; Gibson 2009 and this volume; Geist 2009; Estes, Grant, and Grant 2000; and Grant and Estes 2009).

[3] The edition of Notebook A edited by S. Herbert is contained in Barrett et al 1987. The transcription by K. Thalia Grant and Gregory Estes of Darwin's geological notes from the Galápagos Islands is available on wwww.darwin-online.org.uk. For views of the permanent exhibit on Darwin's geology that feature a selection of the specimens he collected during the voyage see "The Darwin Collection" at <*www.sedgwickmuseum.org*>

[4] A special issue of *Revista Asociación Geológica Argentina* devoted to "Darwin en Argentina," with eighteen articles in English, was published in February 2009. The first article surveys Darwin's work in the region (Aguirre-Urreta, Griffin, and Ramos 2009). The issue is available at <*www.darwin-online.org/uk*>.

[5] McBirney and Williams 1969:54: "Special effort was made to find the soda trachyte reportedly collected by Darwin from James Island and carefully described by Richardson (1933), but we found nothing remotely resembling this unusual rock. Dr. S.O. Agrell furnished us with a thin section of Darwin's specimen, now in the Sedgwick Museum, Cambridge, and this is almost identical with the specimen meticulously described by Richardson. It is, however, quite unlike any rock we found in the entire archipelago; hence, until the presence of trachyte on James Island is confirmed, we cannot exclude the possibility that the specimen described by Richardson was erroneously included in Darwin's collection." During the 2007 expedition our team was able to confirm the existence of trachyte on James Island (Isla Santiago) (Herbert 2009 et al.; Gibson 2009).

[6] George Peacock to J.S. Henslow, 6 or 13 August 1831; J.S. Henslow to C. Darwin 24 August 1831, C. Darwin to J.S. Henslow, 9 September 1831 in Burkhardt et al., 1985, 1:127–129, 149.

[7] Henslow's extensive comments on collecting practice are from the letter, his first, he wrote to Darwin in January 1833. Darwin did not receive that letter until 1834. Darwin's letters, to which Henslow was replying, date from 18 May–16 June 1832 and 23 July –15 August 1832. For the Darwin-Henslow exchanges consult the index to Burkhardt et al., 1985, *Correspondence of Charles Darwin* 1.

[8] A "collection" indicates a specimen or specimens of the same plant collected at the same site at the same time. At James Island (Isla Santiago) Darwin collected 83 species, 42 of them new, five bearing his collecting numbers (85 collections; 129 herbarium sheets, 77 of which are type specimens) (Porter this volume). See also Porter 1980, 1982.

[9] As an example of one outlier collection, Dr. Mike Howe, Chief Curator of the British Geological Survey, recently drew attention to the existence of some geological specimens from the *Beagle* voyage (105 specimens from Ascension Island, presented by Darwin and Captain Ord, R.E. and 10 specimens from Chatham Island in the Galápagos Islands collected and presented by Darwin alone) that were deposited at the Museum of Economic Geology. See Ramsay, Bristow, Geikie, and Bauerman 1862.

[10] For more caveats see Fagan 2007:617. The geological specimens formed part of a collection of specimens stored dry. However, they had their own catalogue. This could be confusing. When delivering the geological specimen catalogue to H. McKinney Hughes in 1897, Francis Darwin wrote "Why it begins at 12 I don't know." (Sedgwick Museum Archive.) The answer to Francis Darwin's query is that numbers 1 through 11 were not geological specimens. (Keynes 2000). The last geological specimen listed in the geological specimen catalogue is 3913 from the Azores. Harker (1907:102) used the figure of 2,000 geological specimens in the collection. In a recent inventory Liz Hide recorded 1371 (of 1930) specimens in the collection (Hide 2007). While preparing for the exhibit on Darwin's geology that opened in July 2009 at the Sedgwick Muse-

um of Earth Sciences, Francis Neary, Project Manager to the exhibit, estimated that about 1,500 specimens would eventually be located at the Museum.

[11] Charles Darwin to John Stevens Henslow, 23 July–15 August 1832 in Burkhardt et al., 1985:250–251.

[12] John .Stevens Henslow to Charles Darwin, 15–21 January 1833 in Burkhardt et al., 1985:292. For a more general discussion of Darwin's treatment of geological speciimens see Herbert 2005, Chapter 3.

[13] John Parker, "Secret Cambridge: The Herbarium." *Cam* 57 (Easter Term 2009):18.

[14] John Parker, "Displaying the Foundations of Evolutionary Thinking." *Research Horizons: The University of Cambridge Research Magazine* 9 (Summer 2009):13. (<*www.research-horizons.cam.ac.uk*>) This article lists 2700 plants as the size of Darwin's *Beagle* collection. The Herbarium sheets holding Darwin's *Beagle* specimens can be viewed at <*www.darwinsbeagleplants.org/Darwin/Home.aspx*>. A recent exhibit catalog emphasizing Darwin's botany is Kohn 2008.

[15] J.S. Henslow to C. Darwin, 15–21 January 1833 in Burkhardt et al., 1985:293.

[16] Charles Darwin to John Stevens Henslow, 28–29 January 1836 in Burkhardt 1985:485.

[17] In the search for a trachyte outcrop to correspond with specimen 3268, several people offered timely assistance. In 1999 Greg Estes and Thalia Grant suggested to me that from their recreation of Darwin's route they could identify the likely site where Darwin had found specimen 3268. This indeed proved to be the case. When Dennis Geist joined the team in 2006, his own knowledge of the literature regarding igneous rocks on the islands yielded a thesis by Hermann Baitis who had found trachytes on Isla Santiago and that these rocks had been analyzed (Baitis 1976; Lindstrom 1976). Thus, when the on-site team began work on the island in the summer of 2007, it was reasonably confident that it would locate Darwin's site and find rocks similar to his. The team did so within a day and half of setting foot on the island, an experience that mimicked Darwin's own. This left the team free to explore and collect on other sites on the island, and for Sally Gibson to survey the whole island from the point of view of its rock diversity (Herbert et al. 2009; Gibson 2009, this volume).

[18] The bracketed word 'acid' as a substitute for trachyte is Harker's addition.

[19] Rudwick 2004; Wilson 1972:164–182, 273–277. Darwin's other main source of information in his contemporary notes on James Island was Charles Daubeny, who carefully distanced himself from Scrope [Daubeny 1826:viii–ix]. On Darwin's relation to Daubeny and Scrope see Gibson this volume.

[20] Grant and Estes 2009 plate 12 (a–d) has photographs of the Galápagos mockingbirds with guides to their distinguishing characteristics. Also note a video of Darwin's actual specimens of the six South American mockingbirds he collected as well as the four Galápagos specimens on (<*www.nhm.ac.uk*>) [accessed January 13, 2010], and a black and white photograph of type specimens for the Galápagos birds (Sulloway 1982, Figure 4). On their importance to Darwin's adoption of an evolutionary scheme see Herbert 1968:73–79; Herbert 1980; and Sulloway 1982. Exhibits honoring Darwin in 2009 at the California Academy of Sciences and at the National Museum of Natural History also focused on the Galápagos mockingbirds. For current views on Galapágos mockingbird classification and phylogeny, see Arbogast (2006) and P.R. and B.R Grant (2008)

[21] Rock types can be named from classic sites where they occur, as, for example, andesite, named in 1836 by Leopold von Buch. See Le Maitre 2004:56, and Herbert et al. 2009:5.

[22] See Figure 9 in Herbert 2009 et al. for a full comparison. These rock samples are on display in the "Darwin's Legacy" exhibit at the National Museum of Natural History through September 12, 2010.

[23] Gould 1837. For treatment of Darwin's interactions with London professionals as regard to his collections see Herbert 1974. See also Sulloway 1982 which includes reproduction of Darwin's notes on his important conversation with John Gould regarding Galápagos birds.

[24] Notebook A, pages 21, 32, 34, and 35 contain discussion of trachytes and basalts. In one comment (A:35) Darwin followed Scrope when asking himself the question (A:35), "Is the feldspar glassy in greenstone dikes which rise through granite — a most important question with respect to my theory of changes of granites into Trachytes.—" The probable date for this entry is late 1837. (Barrett et al. 1987) As Sally Gibson has pointed out (this volume), by the time Darwin wrote *Volcanic Islands* he had abandoned the notion (which Scrope held) of granite as the source for trachyte.

[25] Darwin 1844:118–119. The B.A.A.S. met in August, but Darwin dated the meeting to September.

[26] Young 2003:125–140, 199–214. James Dwight Dana was an important early advocate of Darwin's coral reef theory. He also referred to Darwin's work on lava separation in a footnote. Although he disagreed

with Darwin about lavas, he did affirm (with qualifications) that "particular rocks have no necessary relation to time on our globe" (Dana 1849:374, 378). Writing nearly thirty years later, Dana's student Clarence King compared Darwin's Galápagos observation on lava separation to his own similar observations in Hawaii and treated the Scrope-Darwin approach of what he termed "specific-gravity separation" with respect, incorporating it into his own hypotheses (King 1878:715–716). Like several other writers King used biologically-attuned vocabulary when he wrote of the "Genesis of Volcanic Species" (p. 705). Writing still later, in the 1890s, Joseph Iddings, representing a new generation of petrologists proficient in geochemistry as well as field work, credited both Scrope and Darwin, but he also noted what he believed were the "crudeness" of their conceptions as compared to those of Dana who had written five years after Darwin. Unlike his English colleagues Iddings did not borrow rhetoric directly from evolutionary theory in describing notions of differentiation (a term he did use). Instead he spoke of the "consanguinity of igneous rocks" — a phrase which could, of course, be easily assimilated to evolutionary rhetoric (Iddings 1892:187, 128).

[27] Scrope was unpersuaded by Lyell's views on metamorphism and on the unrecoverability of the earliest-formed strata on the earth: "Undoubtedly, we should not be warranted in *assuming* that we have discovered, or shall ever discover and identify, the first formed strata; but we may surely seek for them without irreverence. If we believed in Mr. Lyell's subterranean cookery of sedimentary strata into granite, we should consider the search [a] hopeless one; but certainly no more a profane inquiry into hidden mysteries than any one of Mr. Lyell's own speculations" ([Anonymous] 1835:447).

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Darwin the Geologist in Galápagos: An Early Insight into Sub-volcanic Magmatic Processes

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In the early- to mid-nineteenth century, the origin and causes of diversity of igneous rocks, such as granite, basalt and trachyte, were of considerable scientific debate: did they form at different times in the Earth's history or were they related to one another by contemporaneous processes? At the onset of the *Beagle* voyage Charles Darwin was interested in the processes that give rise to the formation of volcanic islands but only possessed limited field knowledge of igneous rocks, and systematic classification schemes had not been fully developed. Despite this, the five weeks that he spent in Galápagos in 1835 were to become highly influential to his understanding of the processes involved in the diversification of igneous rocks. Of especial importance were Darwin's observations and specimens from Isla Santiago (formerly known as James Island), the island where he collected the widest variety of igneous rocks during the *Beagle* voyage.

Darwin's geological notes from Galápagos suggest that he initially classified most of the feldspar-rich lavas as trachytes and those containing olivine as basalts. Recent geochemical analyses of some of his Galápagos specimens have confirmed that only one is in fact a 'true' trachyte. This must have come from a small outcrop near the summit of Santiago, the only island in Galápagos which he visited where trachyte occurs. On the basis of his observations on Santiago, together with those subsequently made on Ascension and Terceira (Azores), Darwin realised that trachytes and basalts could be erupted from the same volcano, i.e., that they formed in the same period of geological time. He further suggested that both trachytes and basalts might be formed by the 'sinking of crystals' from the same body of 'liquified volcanic rock'. Darwin's ideas were not widely accepted by mid-nineteenth century scientists who predominantly believed that trachytes and basalts represented different 'series' of igneous rocks and that trachytes formed by melting of granites. It was only in the early 20th century that theories involving density settling of minerals as a cause for the compositional diversification of igneous rocks became in vogue; these now form the basis of our current understanding of sub-volcanic magmatic processes.

Introduction

HMS *Beagle* entered the waters of the Galápagos archipelago on the 15th of September 1835, over 3½ years after leaving England. Captain Robert Fitzroy (1805–1865) and his men had spent much of this time surveying the coastline of South America for the Admiralty (Fig. 1) but were also engaged in recording the shape and slope of coral islands, in order to provide information that might test a recently proposed theory that they were underlain by volcanoes. On board HMS *Beagle* was Charles Darwin (1809–1882), the ship's unpaid naturalist.

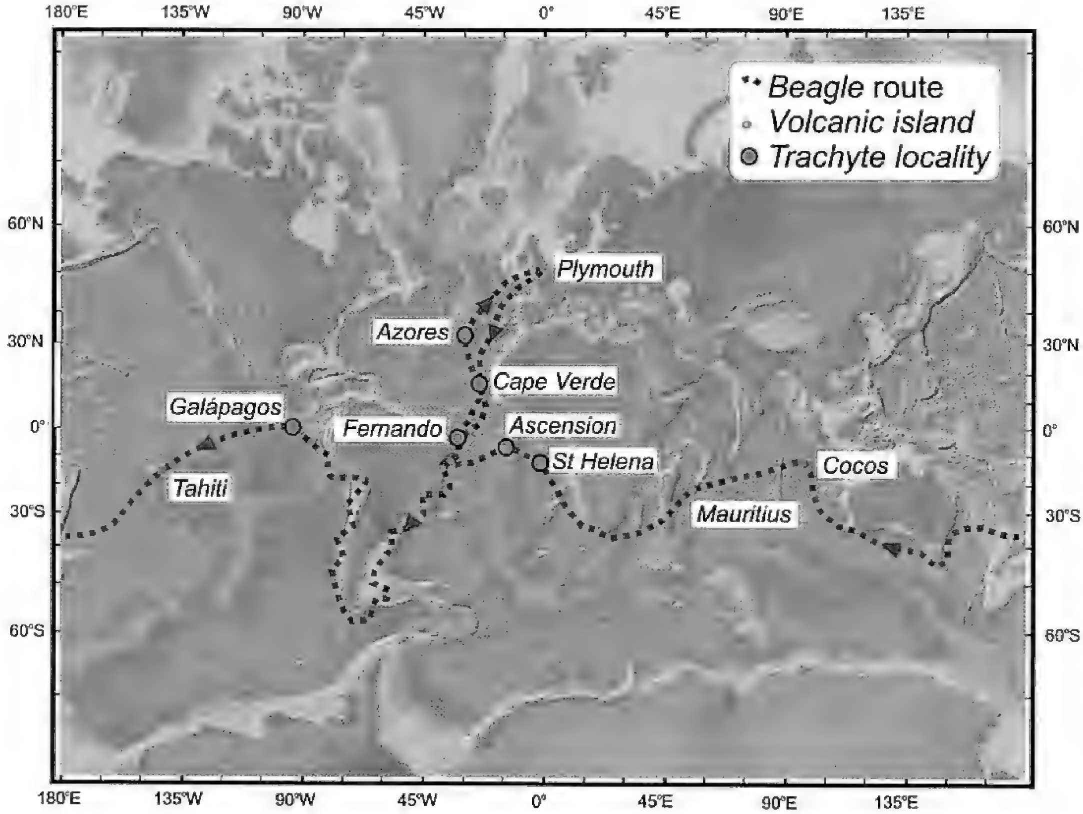

FIGURE 1. Route of the *Beagle* between 27th December 1831 and 2nd October 1836. Small closed circles illustrate locations of volcanic islands that Darwin visited during the voyage. Those shown by larger circles are where Darwin may have encountered trachytes. Base map showing bathymetry and topography is from GEOMAPAPP.

Darwin had become interested in geology and chemistry during his childhood and subsequently attended lectures on the subjects by Robert Jameson (1774–1854) and Thomas Hope (1766–1844), whilst studying medicine at the University of Edinburgh (1825–27). Darwin later moved to the University of Cambridge (1828–1831) where he took what was then the standard academic undergraduate course. During this time, he was closely supervised by John Stevens Henslow (1796–1861) — a botanist (see Porter, this volume) and former Professor of Mineralogy — who encouraged him to study geology and also introduced him to the Woodwardian Professor of Geology, Adam Sedgwick (1785–1873). Darwin accompanied Sedgwick into the field in August 1831 and gained invaluable training in field geology. Shortly after, he was invited to join the *Beagle* voyage as the ship's naturalist. At this stage in his career Darwin was fascinated by geology (Secord 1991; Herbert 2005) and — inspired by Alexander von Humboldt's *Personal Narrative* (1799–1804), which contained a detailed account of the geology of the Canary Islands — keen to find out more about the formation of volcanic islands. It was Darwin's visit to the Galápagos archipelago in 1835, however, that was to be pivotal to his understanding of volcanic processes.

Sedgwick recommended that the principle book Darwin should take on board the *Beagle* was *A description of active and extinct volcanos* [sic] by Charles Daubeny (1826) together with *Traité de Géognosie* by Jean-Francois d'Aubuisson de Voisins (1819) and von Humboldt's *Personal Narrative* (1799–1804). He is known to also have had a copy of *Considerations on volcanos* by George Poulett Scrope (1825) and *Principles of Geology* by Charles Lyell (1830–1833), which were both

recommended by Henslow[1]. All of these publications appear to have significantly influenced Darwin's understanding of igneous rocks on the *Beagle* voyage. At the onset of the voyage he would only have had limited knowledge of the field identification of igneous rocks in the field, gained on trips to outcrops of basalt and dolerite at Salisbury Crags (Edinburgh) and granites on Exmoor in SW England (Secord, 1991). By the time of the *Beagle's* arrival in Galápagos, Darwin would have visited the volcanic islands of Cape Verde (16th January–7th February 1832) and Fernando de Norohna (20th February 1832) and also have seen volcanic rocks in southern Brazil and the Andes (Fig. 1)[2]. Darwin's observations on these recently active volcanic islands increased his belief that currently active Earth processes may have been operational in the past and convinced him of the 'superiority' of Lyell's views.

Early- to mid-nineteenth century understanding of volcanic rocks

By the late-eighteenth century scientists had realised that, in order to understand the complexity of volcanic phenomena and how these contributed to general theories of the Earth, it was important to undertake scientific travel and comparative study of different volcanoes (Rudwick 2005; Vaccari 2008). Primarily, these investigations involved field trips to recently active volcanoes in southern Europe, such as Etna and Vesuvius, where scientists made detailed observations and collected specimens of rocks and minerals. In some cases these specimens subsequently formed the basis of experiments, which were undertaken in order to determine both the physical and chemical properties of volcanic rocks and the minerals which they contained, e.g., Spallanzani (1729–1799).

Of specific interest to European scientists during the early 1800s was the origin of basalt and how this might be related to other types of igneous rock, such as granite and trachyte. These were not simply provincial interests but concerned the origin of igneous rocks across Europe and subsequently the globe. Some British scientists — including William Buckland (1784–1856), Charles Daubeny (1795–1867), George Poulett Scrope (1797–1876) and Sedgwick — had started to dismiss the widely-established Wernerian 'Neptunian' hypothesis[3], which inferred that not all basalts were volcanic and some had precipitated from a large primeval ocean of water. Wernerian scientists believed that rocks were characteristic of different geological periods and those such as granite and gneiss were generated early in the Earth's formation (i.e., were 'primary' strata) followed by trachyte ('secondary strata') and then basalt ('tertiary strata')[4]. The geological age of a rock thus became a major factor in classification especially to scientists in continental Europe.

Scrope published a full length account of volcanoes in the English language in 1825 entitled *Considerations on volcanos*. At the time, his ideas were regarded as radical, especially those relating to formation of different rock types at the same period of geological time. Scrope was especially critical of the Wernerian approach and was later to write of the scientific discord that existed in ~1820:

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[1] Both of these publications were regarded as radical at the time of their publication especially by Adam Sedgwick.

[2] Darwin's visit to the Canary Islands was prevented by quarantine restrictions following an outbreak of cholera in England.

[3] Named after Abraham Gottlob Werner (1749–1817) who was a German geologist.

[4] In the early 1800s, the terms granite and basalt had long been in use: initial uses of the terms 'basalt' and 'granite' have been attributed to Pliny (77AD) and Caesalpino (1596), respectively (Le Maitre 2002). Trachyte (derived from the word *trachus* meaning rough) was first used by Haüy (1743–1822) in the late 1700s to describe rocks from the Drachenfels region of the Rhine. The word trachyte came into more general use following publication of *Essai d'une Classification Mineralogique des Roches Mélanges* (1813) by Alexandre Brongniart (1770–1847), who succeeded Haüy as professor of mineralogy in the Museum of Natural History in Paris, and *Voyage Mineralogique et Geologique en Hongrie* (1822), written by Haüy's former pupil François Beudant (1795–1867).

> . . . the error of the Wernerians in undervaluing, or rather despising altogether as of no appreciable value, the influence of volcanic forces in the production of rocks that compose the surface of the globe, formed a fatal bar to the progress of sound geological science, which it was above all things desirable to remove. (Scrope 1858.)

Scrope's (1825) publication was closely followed by *A description of active and extinct volcanos by Daubeny* (1826) who referred to similar volcanic regions of Europe (including the active volcanoes of Vesuvius and Etna and extinct volcanoes in the Auvergne and Ardàche regions of France, Lower Rhine in Germany and Hungary). Scrope's views are thought to have influenced those of Charles Lyell (1797–1875) and both shared the view that the 'present was the key to the past'. In contrast, Daubeny, who had been a student of Jameson (a firm advocate of Wernerianism), remained convinced that trachytes were formed at a different period in the Earth's formation from basalts.

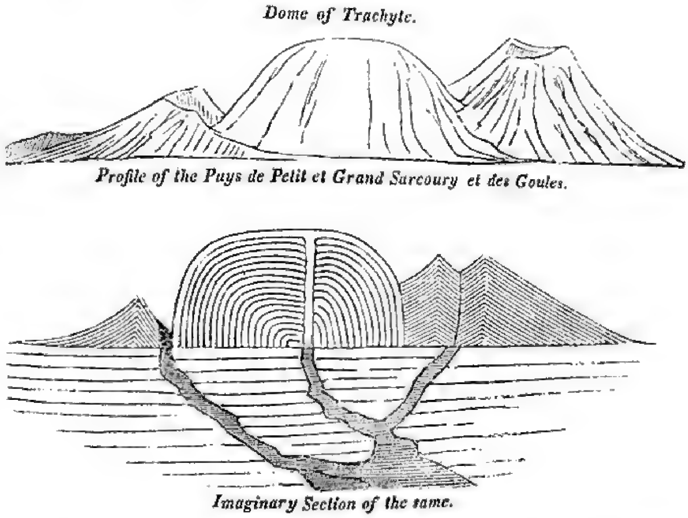

FIGURE 2. Sketches of volcanic phenomena in the Auvergne. Reprinted and modified from Scrope (1825, 1827). This region was the main focus of debate regarding the origin of basalt and trachyte in the early 19th century. The sketches show a central dome of trachyte surrounded by basalt. The image is published with permission of the *Geological Society of London*.

Whilst Daubeny (1826) focused primarily on the chemistry of volcanic rocks[5], Scrope (1825) was interested in their physical properties and attributed the typical field occurrence of basalts as thin lava flows and trachytes as domes to their relative fluidity (Fig. 2). Scrope proposed that this was a direct consequence of basalts and trachytes having flowed over the surface of the Earth, a view that contrasted with those of Wernerian scientists, such as Leopold von Buch (1774–1853) and von Humboldt (1769–1859), who believed that lavas represented 'craters of elevation' that were inflated from below in a catastrophic manner. Scrope wrote:

> . . . that the lavas which are mineralogically classed as basalts from the prevalence of the ferruginous minerals — augite, hornblende, or titaniferous iron in their composition,—are almost universally found to have spread into thin *sheets*, or long and shallow *currents*, to a considerable distance from the orifice of protrusion;—while those lava-rocks which consist almost wholly of felspar (trachytes) are as uniformly disposed in massive beds, hummocks, or domes. . . .
>
> This so remarkable and constant relation between the mineral nature of a bed of consolidated lava and the proportions of its different dimensions, has been already recognized by Geologists ; but many have been unfortunately led by this remark to the adoption of a serious error as to the origin of the trachytic and phonolitic rocks, which are considered by them as in no instance to have flowed on the surface of the earth, but to have been always elevated en masse into the position they now occupy. . . .

[5] Daubeny was Professor of Chemistry at the University of Oxford

> Some writers have even gone the length of supposing that they swelled up like a bladder by inflation from below, (De Buch, Humboldt,) and are consequently still *hollow within*—a gratuitous supposition entirely at variance with all that we know for certain concerning the nature and mode of operation of the volcanic energy. . . .
>
> It is on the contrary obvious that the remarkable bulkiness of the felspathic lavas is fully and simply accounted for by their imperfect fluidity, which has been already recognised to diminish, ceteris paribus, with their specific gravity, and by no means induces the necessity of supposing any other mode of volcanic action than that by which the basaltic lavas were also produced. (Scrope 1825:92–94.)

In addition to describing the physical and chemical properties of volcanic rocks of Europe both Scrope (1825) and Daubeny (1826) also gave brief descriptions of the geology of volcanic islands in the Atlantic and Pacific Oceans. The latter were based on the accounts of travellers and scientists; the Galápagos, however, only merited a single cursory remark:

> . . . to the numerous groups or systems of volcanic vents which are observable on the globe. Of these, some are united into clusters or detached irregular groups, the position of each vent bearing no very apparent relation to that of the others; such as those of Iceland, the Azores, Canaries, and Cape Verd Isles in the Atlantic; and the Archipelagos of the Moluccas, and Gallipagos, in the Pacific &c. (Scrope 1825:186.)

The geology of the Galápagos was largely unknown in the early nineteenth century since the main visitors to the islands, following their discovery in 1535, were buccaneers, pirates, warships, whalers and explorers (Rose 1933; Larsen, this volume). Nevertheless, Darwin would have been conscious of the volcanic landscapes in the Galápagos archipelago, from descriptions given by William Dampier and James Colnett, and may also of have been aware of volcanic eruptions on Albemale (Isabela) and Narborough (Fernandina) in the early 1800s after reading the works of Captain David Porter, Captain Asano Delano and Admiral George Byron (Larsen, this volume). Unfortunately, there were no eruptions whilst Darwin was in Galápagos, but his observations of 'ancient' craters and distribution of volcanic rock types were key to his subsequent understanding of the processes involved in the formation of basalts and trachytes.

Darwin's geological specimens from Galápagos

The *Beagle* chartered the coast lines of the volcanic islands that constitute the Galápagos archipelago between September 17th and October 20th in 1835 (Fig. 3). Darwin spent about nineteen of these days ashore, visiting the islands of Chatham (now known as San Cristobal), Charles (Floreana), Albemarle (Isabela) and James (Santiago). During this time he collected 31 specimens of igneous rocks, which are now housed, together with ~1500 of Darwin's other geological specimens from the *Beagle* voyage, in the Harker collection of the Sedgwick Museum at the University of Cambridge (F. Neary, pers comm.). Those from Galápagos have the label CD32**[6]. Four of the geological samples in Darwin's Galápagos collection are of lavas from islands in the northern part of the archipelago (Marchena, Genovesa and Pinta, Fig. 3) and were collected by Chaffers whilst Darwin was on Santiago. They nevertheless bear Darwin's samples numbers (CD3286–3289) and were described by him in his specimen notebook[7].

Most of the geological specimens in Darwin's collection from Galápagos consist of consolidated volcanic rocks taken from lavas together with a few dykes, tuffs (known to Darwin as vol-

[6] Two samples are missing: a 'fragment' (i..e., a gabbro) from Santiago (CD3274) and a basalt from Genovesa (CD3288).

canic 'sandstones') and plutonic rocks. Thin sections of the crystalline igneous rocks were made by Alfred Harker (1859–1939) and subsequently became the focus of a project by Constance Richardson (1907–1989) in 1933. More recently, Pearson (1996), Herbert (2005), Herbert *et al.* (2009) and Gibson (2009) have examined some of the geological specimens from Santiago. The latter represent by far the majority (nineteen) of the volcanic rock specimens in Darwin's collection from Galápagos and are the most varied. Isla Santiago was the last island that Darwin visited in the archipelago and where he spent the most time (ten days). He landed with his party of men in the northwest of the island where there were known to be intermittent supplies of fresh water. He spent only a few days at the beginning of his visit (8th October–11th October) collecting geological specimens (Herbert et al. 2009). The rest were engaged in obtaining botanical (see Porter, this issue) and zoological specimens. Darwin is known to have collected rock samples from Buccaneer Cove (Freshwater Bay; Fig. 4), went on a two day hike to the 2950′ summit of the island, and also accompanied some of the resident tortoise hunters on a boat trip down the coast to James Bay (Fig. 5, see Gibson 2009; Herbert et al. 2009).

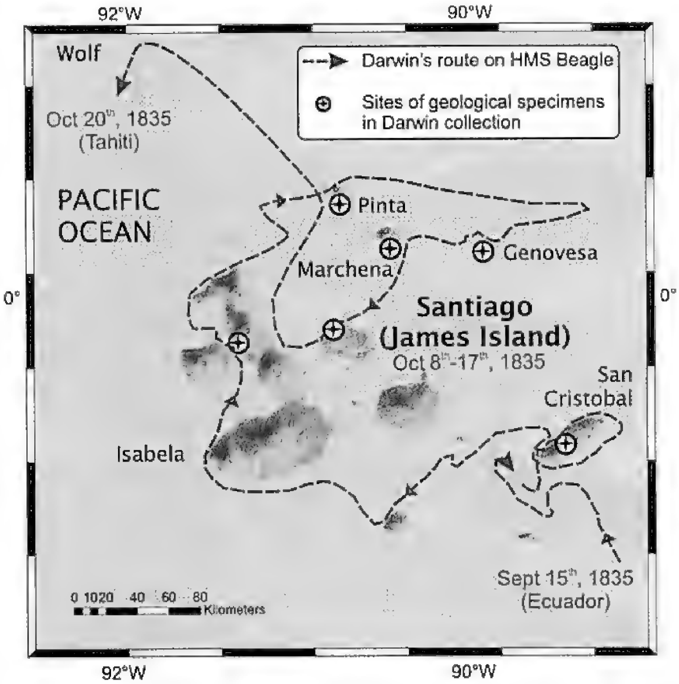

FIGURE 3. Route of the *Beagle* in the Galápagos archipelago. Also shown are the sites of samples currently in the Harker collection of the Sedgwick Museum, University of Cambridge. Note that samples from Pinta, Marchena and Genovesa were collected by Chaffers (DAR 37.2:784).

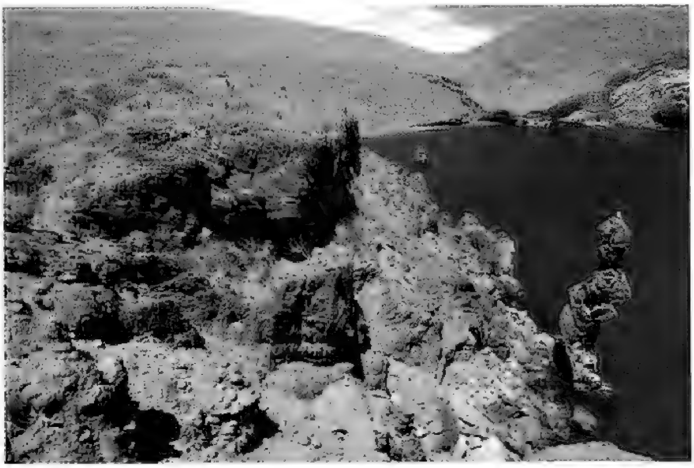

FIGURE 4. Buccaneer Cove (known to Darwin as Freshwater Bay) where Darwin and his party of men landed on Isla Santiago on 8th October 1835. Image courtesy of A. Thurman.

Darwin collected both plutonic and volcanic rocks from Santiago: one of the most striking

[7] A further set of samples from San Cristobal were given by Darwin to the British Geological Survey for an exhibit in 1858; these have inscriptions from Darwin (M. Howe, pers comm.) but do not seem to have been registered in his specimen notebook. The Survey records show that many of these were collected from wells on San Cristobal and the samples may perhaps have been donated to Darwin after the *Beagle* voyage.

aspects of these is their diversity and it seems that, like any skilled collector, he was keen to procure as many different types of igneous rock as possible (see Herbert, this volume). In hand specimens, these differences are very subtle but would have been more apparent to Darwin on an outcrop scale. The coarse-grained (>2 mm) plutonic rocks (described by Darwin as 'fragments' in *Volcanic Islands*, p.239) show variations in the amount of dark-coloured (mafic) minerals, such as olivine and pyroxene (augite) and light-coloured (felsic) minerals, such as feldspar, and were initially incorrectly described by Darwin as granite (Pearson 1996). These coarse-grained igneous rocks were collected from the 'wreck of an ancient crater' which forms the promontory at the north end of Buccaneer Cove. The rocks are highly reddened because of hydrothermal activity associated with the crater: if Darwin had ventured a few hundred meters around the northern side of the promontory he would have found much fresher examples that would have provided him with important evidence as to their relationship with the host lavas (Gibson 2009). Darwin collected these 'fragments' after he had taken a long south-east inland traverse to the highlands of Santiago and obtained samples of 'trachyte' and 'trachytic' rocks (Herbert et al. 2009). At this point in the voyage, he would almost certainly have been aware of Scrope's hypothesis that trachytes formed by melting of granite and his initial misidentification of these rocks as granite may also have been influenced by his reading of Daubeny (1826) who wrote of the Puy Chopine in the Auvergne:

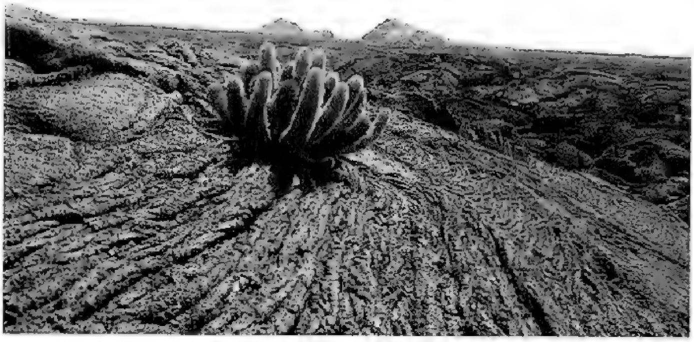

FIGURE 5. A basalt lava flow at James Bay (known to Darwin as Puerto Grande) visited by Darwin on 11th October 1835 and described by him as '*Surface ringed, (like Cow-dung), which often takes form of cables…*'. Image courtesy of A. Thurman.

> On climbing to the summit, I found, *in situ*, a rock analogous to domite[8], unaltered granite, and a conglomerate with a granitic base, rocks which seem to be related to one another. Lower down I observed a granular hornblende rock, which appeared to pass into granite; and these four substances make up, so far as my observations extend, the higher portions of the mountain. Lower down, we have lavas, both compact and vesicular, none of which, so far as I observed, occupy the summit. (Daubeny 1826:18.)

Darwin's evolving nomenclature for Galápagos rocks

Darwin's field notes of volcanic rocks in Galápagos are descriptive and provide only a few details of where specimens were collected. Emphasis was placed on the colour of the rocks, presence of olivine or feldspar and whether or not they are compact or 'cellular' (i.e., vesicular). In his field notes he wrote of Santiago:

> Stream.— Have burst from several small Craters at foot of central Trachytic mass of highest hills & Craters.— Consists of Greystones such as (3280) which abounds in a very remarkable degree, with quantities of olivine. Is generally very Vesicular & sometimes

[8] Domite was the name given by early nineteenth century scientists to a variety of altered, light-coloured trachyte containing mica and occasional quartz.

> rather a Darker color (3281).— The Basis is much the same as in Central Trachytes, the Olivine here replacing glassy Feldspar.— Its surface is smoother than the Basalt of Chatham Isd.— Yet many great fissures.— Surface ringed, (like Cow-dung), which often takes form of cables; folds in a [*illegible*] & branches with rough bark. In this Island we have this Olivine Lava as the latest, whilst in Albemarle, that of Trachyte.— Near to the Sea, it has burst through an ancient crater, (composed of igneo-cemented red glassy Scoriae & greystone Lavas) filled up Crater & left only 2 pieces, which stand in front of each other.— (DAR 37.2:722.)

Then, as now, understanding the causes of formation of igneous rocks relied on the consistent use of a common language for rock nomenclature. Much of this was based on outcrops in Europe and not always appropriate for rocks in other parts of the globe. The rock nomenclature that Darwin adopted during the *Beagle* voyage was more generic than that given in his subsequent publication (Table 1).[9] In his field notes he refers to samples containing abundant 'glassy' feldspar as 'trachyte' or 'trachytic' and all others as 'basalt'. This corresponds with the definitions of the time, including Daubeny (1826) who described trachyte as:

> . . . from the harsh and earthy feel it often possesses, has been denominated trachyte, is essentially composed of crystals of glassy feldspar, often cracked, which are imbedded in a basis generally considered as being itself a modification of compact feldspar. To this are sometimes superadded crystals of hornblende, mica, iron pyrites, specular iron, and more rarely augite, and magnetic or titaniferous iron ore. (Daubeny 1826:7.)

And basalt as:

> . . . consisting essentially of augite, feldspar, and titaniferous, or magnetic iron ore, generally accompanied with olivine, and occasionally with hornblende. In many of these cases the ingredients are too intimately mixed to allow of our ascertaining their nature . . . But it is always easy to distinguish this kind of volcanic product from trachyte, which even when it has the colour of basalt, melts before the blowpipe into a white enamel, whilst the latter retains its original colour after being fused. (Daubeny 1826:7.)

This interpretation is corroborated by comments on the facing page of Darwin's specimen notebook, written in different ink and believed to have been made by him at several later dates (Herbert 2005). Against specimen 3280 and 3266 Darwin wrote '*with olivine base as in foregoing Trachytes. Daubeny state P93. that Olivine is never found in Trachyte. This is an important point*'. He had clearly realized that he was incorrect in classifying an olivine-bearing rock as a trachyte. In smaller handwriting and another different ink, and presumably written at a later date, '*melts dark green*' is added to the facing page of the notebook. This indicates that Darwin was using his blow pipes[10] to establish the types of volcanic rocks that he had collected from Isla Santiago and was not solely reliant on their crystal content. Blow pipes are known to have been on the board the *Beagle* (Secord 1991; Herbert 2005) and Darwin may well have used them whilst still at sea.

After collecting geological specimens in Galápagos, Darwin also became aware of the importance of mineral composition (especially that of the 'glassy' feldspars) in determining the type of volcanic rock in which they occurred. This 'new' line of scientific enquiry may have been influ-

[9] It should be noted, however, that deciphering the modifications made from his field notes is difficult because Darwin does not refer to individual specimens in *Volcanic Islands*

[10] Blow pipes were in common use by scientists in the early-nineteenth century. von Humboldt refers to using one on the isle of Bourbon in *Travels to the Equinoctial Regions of America* (1799–1804). Darwin is thought to have used a blow pipe in his teenage years to test the composition of minerals (Secord 1991). At the time of the *Beagle* voyage, trachytes were known to fuse to a white enamel whereas basalts went black (see Daubeny 1826:101).

TABLE 1. Definition of trachyte, as used by different scientists, before and after the *Beagle* voyage. Note that the most important modification involves the specification of the type of feldspar.

	Physical properties of rock	Essential minerals	Accessory minerals	Origin
Haüy (Late 1700s)		Glassy feldspar		–*
Brongniart (1813:45)	Type of porphyry with a fusible, siliceous base	Glassy feldspar		–*
Beudant (1822)	Fuses to a white enamel. Paste typically black or brown Divides trachyte in to 5 species (see Daubeny 1826, p. 101)	Glassy feldspar	Mica, hornblende	
Scrope (1825:85)	Harsh texture Divides the rock type into a coarse grained 'Common trachyte' and 'Trachytic porphyry'	Almost entirely feldspar	Quartz, mica, lesser amounts of augite and titaniferous iron	Melting of granite
Daubeny (1826:7, 93)	Harsh earthy feel, carified and cellular aspect, porphyritic	Glassy feldspar, often cracked	Feldspar, hornblende, mica, iron pyrites, specular iron, augite, magnetitic or titaniferous iron ore	Melting of greenstone porphyry
Darwin (1835)	Blackish grey, greenish grey	Glassy feldspar		
Von Buch (1836:170)	Light grey with fine grains, splits into slates. Specific gravity of 2.47	Feldspar is lamellar in shape, unbroken and hemitropic (i.e. possesses simple Carlsbad twins).	Iron oxide. Hornblende	
Darwin (1844: 245)	Specific gravity of 2.45. Pale colour.	Chiefly consists of feldspar ('orthite' or 'potash' rather than 'albite')	Hornblende, iron oxide, augite.	By separation of crystals in a 'body of liquified volcanic rock'

*Both Haüy and Brongniart were concerned only with the mineralogical composition of rocks and not their origin.

enced by his reading of '*Description physique des îles Canaries, suivie d'une indication des principaux volcans du globe. . . .*' by von Buch (1836), which was published after Darwin had returned to England. In this account von Buch describes the occurrence of various types of volcanic rocks together with details of their mineral composition. Of particular relevance are his attempts to differentiate hornblende-bearing volcanic rocks found in the Andes (i.e., andesites) from those that he had observed in the Canary Islands; von Buch was more specific than Daubeny (1826), Scrope (1825) and Lyell (1835) and defined trachyte as:

> . . . light grey with fine grains and splits into slates. The feldspar that is present in trachyte is lamellar in shape and the crystals are not broken apart and most of them are hemitropic[11] and analogous to those of Carlsbad. (Translated from French, von Buch 1836:170.)

And andesite as:

> . . . a mixture of crystals of white albite and some more pronounced and glistening crystals of amphibole and mica. (Translated from French, von Buch 1836:480.)

Von Buch's definition of trachyte is similar to that currently in use by igneous petrologists who apply the term to fine-grained volcanic rocks consisting mainly of sanidine (or glassy orthoclase) feldspar. The composition of the feldspar is used to distinguish the rocks from oligoclase- and quartz-trachytes and other intermediate forms. Darwin clearly became concerned about his use of nomenclature for feldspar-bearing volcanic rocks and in Chapter III of *Volcanic Islands* he specifically refers to discussions on the composition of feldspars in volcanic rocks from Ascension with William Hallowes Miller (1801–1880), the Cambridge Professor of Mineralogy. In the early 1800s the type of feldspar was estimated by measuring the angle of intersection of the cleavage planes in the feldspar and when describing a basalt lava flow from Galápagos in a subsequent chapter Darwin stated that:

> I may here remark, that in all these cases, I call the feldspathic crystals, "albite," from their cleavage-planes (as measured by the reflecting goniometer) corresponding with those of that mineral. As, however, other species of this genus have lately been discovered to cleave in nearly the same planes with albite, this determination must be considered as only provisional. I examined the crystals in the lavas of many different parts of the Galápagos group, and I found that none of them, with the exception of some crystals from one part of James Island, cleaved in the direction of orthite or potash-feldspar. (*Volcanic Islands*, p.104.)

It is not clear exactly where on Santiago (James Island) Darwin is referring to in the last sentence of this paragraph. Examinations of Harker's thin sections of his geological specimens from the island have revealed that the only one which contains crystals of alkali feldspar is a greenish-grey lava (CD3268; Fig. 7). The feldspar crystals are very small (~ 1 mm) and it would be difficult to distinguish between "albite", "orthite" or "potash" feldspar with the naked eye or hand lens: techniques involving the use of thin sections to identify minerals were invented in 1850[12]. Furthermore, it seems that after looking at some of the large-feldspar-bearing rocks from Isla Santiago, Darwin realized that although they had a trachytic texture (i.e., where feldspar is the predominant phase over olivine and pyroxene[13]) they could not strictly be classified as trachytes because they contained plagioclase (known to Darwin as "albite") rather than alkali ("orthite" or "potash") feldspar[14]. This fact, together with the dark-green or black colour of the enamel to which the rocks fused, appear to have changed his terminology for the large-feldspar bearing lavas (some of those from Isla Santiago are shown in Fig. 6) and Darwin reclassified most of the specimens in his collection from Galápagos as basalts. For example, in his field notes Darwin wrote of the spatial variation in volcanic rock types:

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[11] Haüy gave this name to crystals in which one half was reversed and cited an example as a twin-crystal of feldspar (see Jameson 1808). This book was heavily revised and the title changed to *Manual of Mineralogy* (1821); a book which Darwin used as a text book whilst in Edinburgh (Secord 1991).

[12] Henry Clifton Sorby (1826–1908) showed in 1850 that by examining thin rock-slices in transmitted light it was possible to find out more about their mineral composition.

[13] Where it [felspar] is in great excess lavas are called trachytic; where augite (or pyroxene) predominates, they are called basaltic (Lyell 1830).

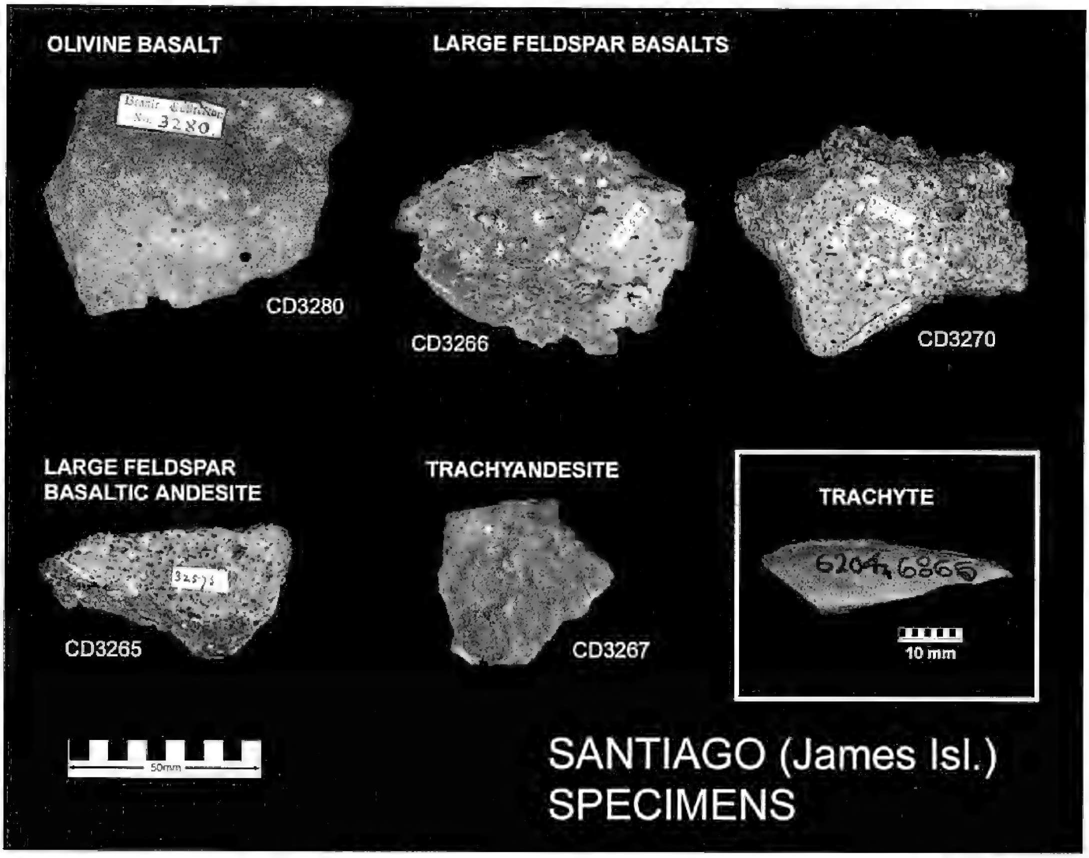

FIGURE 6. Images of some of Darwin's geological specimens from Isla Santiago (known formerly as James Island), courtesy of D. Simmons.

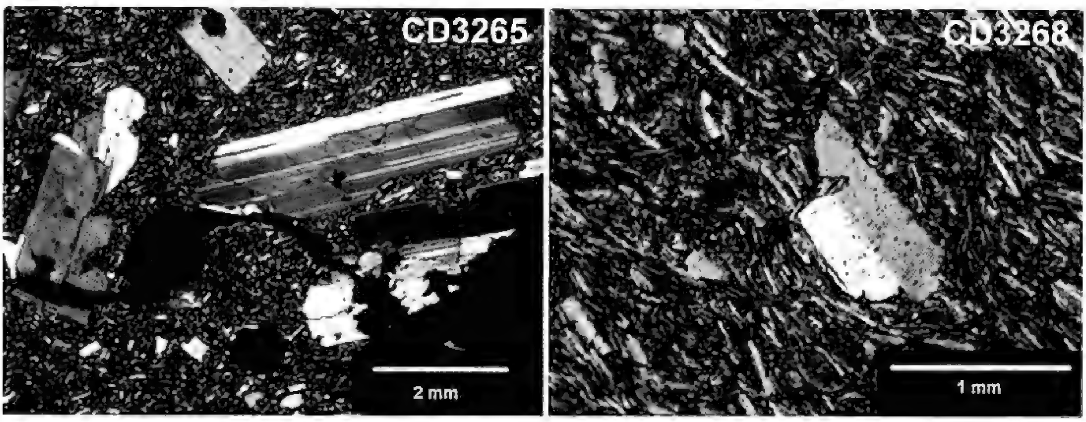

FIGURE 7. Images of feldspars in CD3265 and CD3268 in thin section. Note the presence of fine-scale parallel (lamellar) multiple twinning in the feldspar in CD3265, which is typical of the plagioclase feldspar series (ranging from anorthite to albite). The simple Carlsbad twin shown by the feldspar in CD3268 is typical of alkali feldspars.

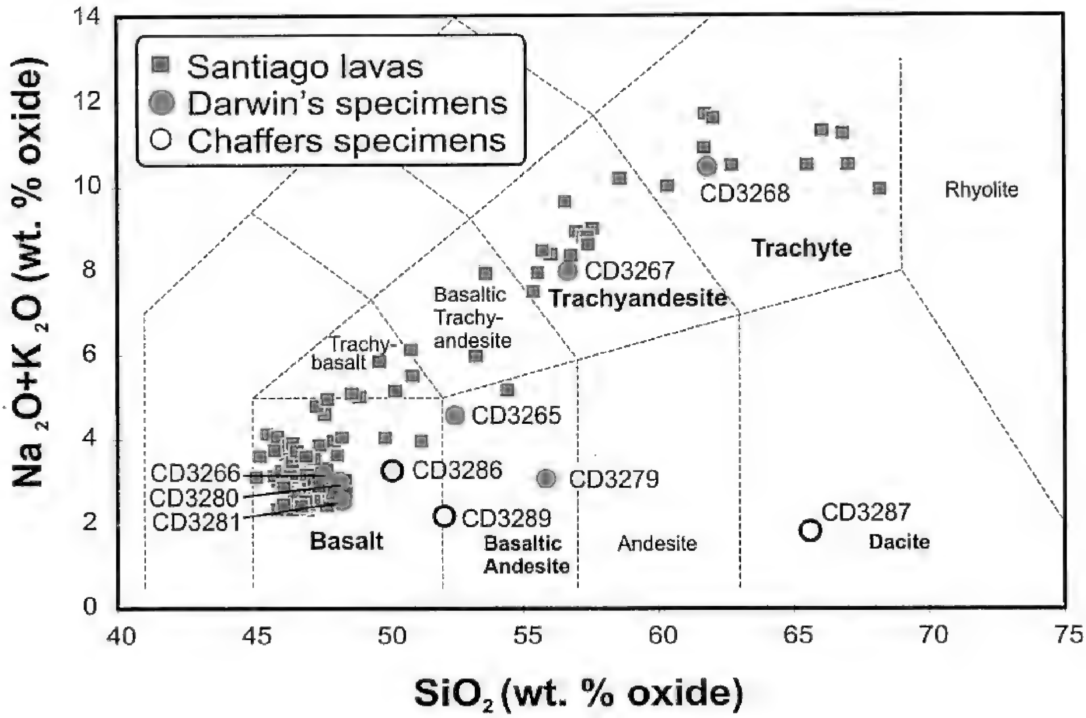

FIGURE 8. Silica versus total alkalis (Na_2O+K_2O) plot showing the wide variety of volcanic rock types present on Isla Santiago (closed squares). Darwin's specimens from Isla Santiago are shown by closed circles. Those collected from the Northern Islands, i.e., Pinta (CD3289), Marchena (CD3286) and Genovesa (CD3287), and given to Darwin by Chaffers, are shown by open symbols. The classification scheme for fine-grained volcanic rocks is from Le Maitre (2002). Data for Santiago are from Baitis (1976), Saal et al. (2007), White et al. (1993) and the author's unpublished data.

> Considering the Islands in the whole archipelago, it may be remarked, that the Southern ones appear to be entirely composed of Basalt & Greystone whilst the Northern division is more essentially Trachytic. (DAR 37.1:786.)

But in *Volcanic Islands* (1844) he described the lavas in the Northern Islands as basalts rather than trachytic:

> In the northern islands, the basaltic lavas seem generally to contain more albite than they do in the southern half of the Archipelago; but almost all the streams contain some. The albite is not unfrequently associated with olivine. I did not observe in any specimen distinguishable crystals of hornblende or augite; I except the fused grains in the ejected fragments, and in the pinnacle of the little crater, above described. I did not meet with a single specimen of true trachyte; though some of the paler lavas, when abounding with large crystals of the harsh and glassy albite, resemble in some degree this rock; but in every case the basis fuses into a black enamel. (*Volcanic Islands*, p 114.)

This modification of rock nomenclature often results in contradictory remarks between Darwin's field notes and *Volcanic Islands*, and almost certainly reflects the confusion amongst early-

[14] Whilst still in use, it has been suggested that the term 'trachytic', which is used to describe the texture (subparallel alignment of lath shaped feldspars) displayed by some volcanic rocks, should be abandoned because it does not always refer to rocks that are classified as trachytes on the basis of their mineralogy and chemical composition (Gillespie and Styles 1999:19).

nineteenth century scientists as to how to classify 'intermediate' volcanic rocks (e.g., Table 1). Accurately distinguishing between different types of volcanic rocks was, however, important to Darwin's understanding of how trachytes and basalts might be erupted from the same volcano.

Chemical classification of Darwin's samples of volcanic rocks from northern and central Galápagos

The petrography of Darwin's samples from Santiago was discussed by Herbert et al. (2009), but in an attempt to apply present-day nomenclature the major-element chemistry of a representative set of his volcanic rocks from Santiago and also the northern islands of Pinta, Marchena and Genovesa has been determined. The specimens were selected on the basis of their wide variation in petrography. A small chip was carefully removed from each sample, ground into a fine powder and then fused into a glass disc. The fusion discs were then analysed by X-ray fluorescence (XRF) at the Open University, UK. Sample CD3268 was analysed in the 1930s and has not been reanalyzed because it is simply too small to yield the several grams necessary for XRF analysis. Nevertheless, it is unlikely that the whole-rock analysis determined by wet chemistry in the 1930s would be significantly different from that by XRF. The whole-rock analyses are presented in Table 2 and

TABLE 2. Location and classification of Darwin's specimens of volcanic rocks from Galápagos referred to in the text

Specimen no.	Location	Darwin's description from his notes	IUGS classification[a]	Preferred classification[b]
CD3265	Santiago	Cellular trachyte (DAR 37.2:786)[c]	–	Large-feldspar basaltic andesite
CD3266	Santiago	Compact trachyte (DAR 37.2:786)[c]	–	Large-feldspar basalt
CD3267	Santiago	Compact trachyte (DAR 37.2:723)[c]	Trachyandesite	Trachyandesite
CD3268	Santiago	Compact trachyte (DAR 37.2:723)[c]	Trachyte	Trachyte
CD3279	Santiago	Compact trachyte (DAR 37.2:772)[c]	–	Large-feldspar basaltic andesite
CD3280	Santiago	Greystone[d] (DAR 37.2:722)[c]	Basalt	Olivine basalt
CD3281	Santiago	Greystone[d] (DAR 37.2:722)[c]	Basalt	Olivine basalt
CD3286	Marchena	Trachyte (DAR 37.2:784)[c]	–	Basalt
CD3287	Genovesa	Very cellular, trachytic (DAR 37.2:785)[c]	–	Large-feldspar basalt
CD3289	Pinta		–	Large-feldspar basalt

[a] IUGS classification is taken from Figure 5.

[b] The preferred classification is based on both the petrographic and chemical characteristics of the specimen.

[c] DAR 37.2 refers to notes written in Darwin's 'Galapagos. Otaheite Lima' notebook.

[d] Greystone was used by Scrope (1825:86) to describe a class of rocks intermediate between basalt and trachyte that have roughly equal proportions of feldspar and ferruginous minerals (i.e. olivine and pyroxene). This term is no longer in use.

TABLE 3. Major-element analyses of a representative set of Darwin's specimens of volcanic rocks from Galápagos

Location	Santiago							Marchena	Genovesa	Pinta
	SE traverse to Highlands			Summit	B. Cove	James Bay	James Bay			
Sample No	**CD3265**	**CD3266**	**CD3267**	**CD3268**	**CD3279**	**CD3280**	**CD3281**	**CD3286**	**CD3287**	**CD3289**
SiO_2	52.43	47.73	56.61	61.9	55.74	48.26	48.44	50.12	65.65	51.5
TiO_2	2.24	2.58	1.38	0.3	1.2	1.94	1.749	2.04	0.96	1.21
Al_2O_3	17.07	15.51	16.51	16.8	12.08	14.6	13.77	14.51	9.65	20.59
Fe_2O_3*	10.72	13.69	9.71	2.3	10.89	12.34	12.09	12.34	7.62	6.23
MnO	0.17	0.2	0.22	0.3	0.15	0.17	0.17	0.19	0.12	0.09
MgO	3.75	7.04	1.51	0.6	7.72	10.32	11.17	7	4.8	4.16
CaO	8.06	10.56	4.41	2.3	7.44	9.47	10.29	11.52	7.98	12.22
Na_2O	3.74	2.97	5.9	7.2	2.62	2.7	2.34	3.06	1.66	2.12
K_2O	0.9	0.28	2.16	3.3	0.52	0.33	0.25	0.24	0.08	0.21
P_2O_5	0.57	0.37	0.56	0.1	0.34	0.25	0.18	0.21	0.27	0.2
LOI	0.94	-0.29	0.97	-	0.45	-0.63	-0.5	-0.32	1.07	1.09
Total	100.57	100.63	99.93	99.69	99.95	99.74	99.95	100.91	99.86	99.61

All samples were analysed by XRF at the Open University (UK) except CD3268 which was analysed by wet chemistry (Richardson 1933). *Total Fe oxide is given as Fe_2O_3.

the widely accepted IUGS chemical classification scheme for volcanic rocks is shown in Figure 8. This classification scheme is used for fine-grained volcanic rocks and not applicable to all of Darwin's samples: those from the northern islands of Pinta (CD3289) and Genovesa (CD3287), given to Darwin by Chaffers, and numerous samples from Isla Santiago (e.g., CD3265, 3266, 3279) contain large rounded crystals of plagioclase feldspar. All of those analysed except CD3265 have MgO contents between 4 and 7 wt. %, which are typical of basalts, and these specimens are best classified as 'large-feldspar' basalts (Table 3). CD3265 has lower MgO (3.75 wt. %) and higher SiO_2 (52.43 wt. %) and is essentially a 'large-feldspar' basaltic andesite. In his field notes Darwin referred to CD3265 and CD3266 as 'highly cellular blackish grey trachyte' (DAR 37.2:723) perhaps because of their high abundance of feldspar. Nevertheless, from the whole-rock chemistry it can be concluded that Darwin collected only a single trachyte (CD3268), together with a trachyandesite (CD3267) and a series of basaltic andesites and basalts (CD3280 and CD3281) from Santiago. Samples CD3280 and CD3281 (Table 3) have relatively low SiO_2 (~48 wt. %) and high MgO contents (>10 wt. %) and may be classified as olivine basalts. Darwin did not specifically discuss the origin of any rocks transitional between basalt and trachyte in either his field notes or *Volcanic Islands* and it is unclear if he attached any scientific importance to the almost continuous spectrum of volcanic rock types that he had

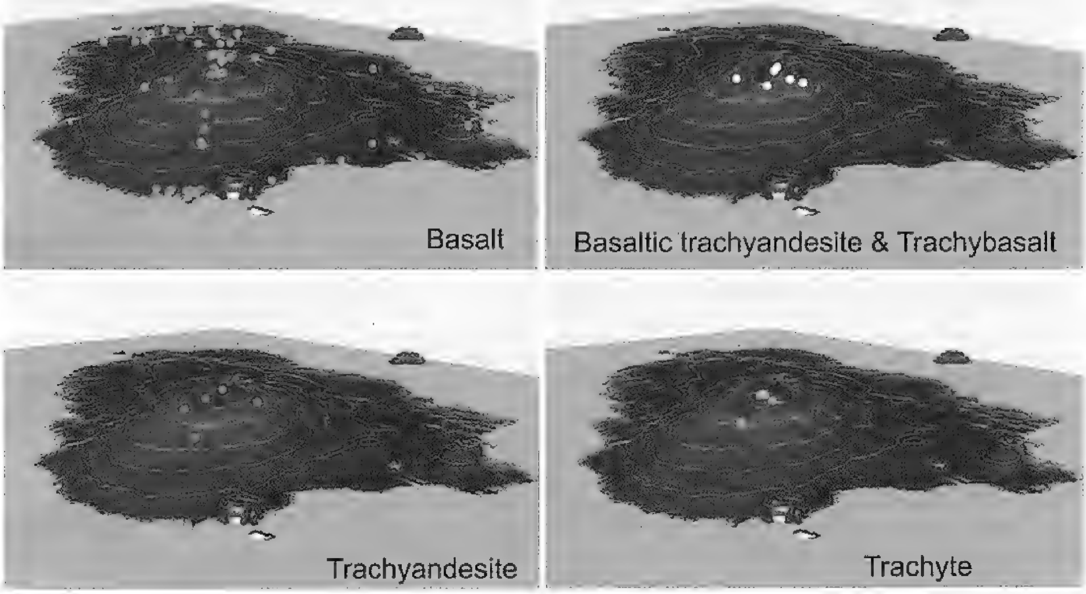

FIGURE 9. Three dimensional digital elevation maps of Isla Santiago showing the locations of different types of volcanic rock as determined by whole-rock silica and total alkali contents. The view of the island is from the west. Contours are shown at 500′ intervals.

observed on Santiago. What is truly remarkable is the wide range of different types of volcanic rock that are present in Darwin's relatively small suite of specimens from Santiago.

Darwin noted that lavas similar to CD3265 were the commonest type that he observed on Santiago. This has been confirmed by recent fieldwork which has shown that 'large-feldspar' basalts are concentrated around the slopes of the large inactive shield volcano that dominates the northwest of Santiago. Olivine basalts are more common in other parts of the island, where they have been erupted from small cones and fissures, and trachyte only occurs in a small outcrop near the summit of Santiago (Fig. 9). The latter is almost certainly the collection site of Dar-

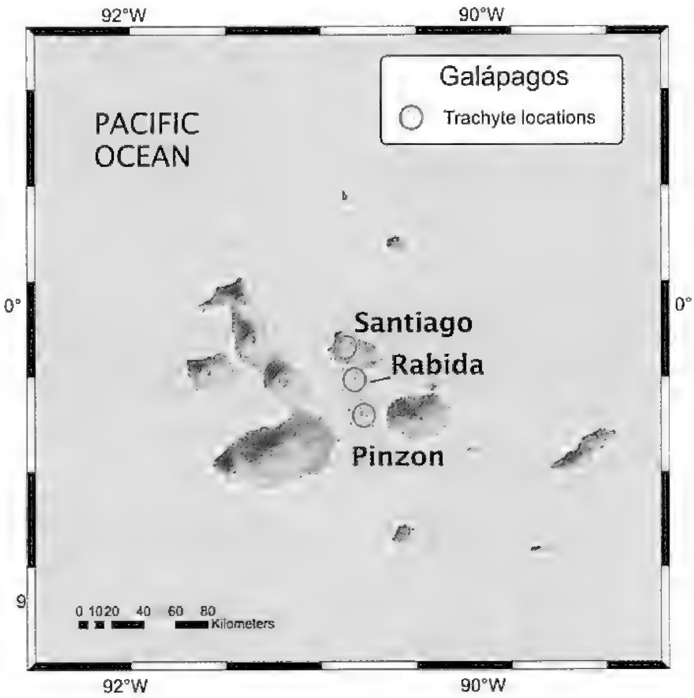

FIGURE 10. Distribution of outcrops of trachyte in the Galápagos archipelago. The information is from the author's unpublished data and Baitis (1976).

win's specimen CD3268 (Herbert et al. 2009; Gibson 2009). This is the single true trachyte that he collected in Galápagos and probably the only one that Darwin observed in the whole of the archipelago: trachyte only occurs at the summit of Santiago, and the small adjacent islands of Pinzon and Rabida (Fig. 10). With the exception of these and Alcedo (on Isabela) all of the other islands in Galápagos have erupted relatively unfractionated basaltic *(s.l.)* magmas. These islands with more evolved magmas are in the centre of the archipelago and, at the time of volcanism, are believed to have resided above shallow, large, long-lived magma chambers with low melt-supply rates. These would have cooled slowly and undergone extensive fractional crystallization (e.g., Geist et al. 1995).

Darwin's basalt-trachyte differentiation theory

After leaving Galápagos the *Beagle* returned to England via islands in the Pacific and Atlantic. During this part of the journey, Darwin observed trachytes both on Ascension and Terceira in the Azores. In Chapters II and III of *Volcanic Islands* (1844) he notes the similarity of the trachytes on these two different islands (p. 24). He also refers to the spatial relationship of the basalt and trachyte on Terceira:

> Many of the basaltic streams can be traced, either to points of eruption at the base of the great central mass of trachyte, or to separate, conical, red-coloured hills, which are scattered over the northern and western borders of the island. (*Volcanic Islands*, p.35.)

And Ascension:

> These occupy the more elevated and central, and likewise the south-eastern, parts of the island. The trachyte is generally of a pale brown colour, stained with small darker patches; it contains broken and bent crystals of glassy feldspar, grains of specular iron, and black microscopical points, which latter, from being easily fused, and then becoming magnetic, I presume are hornblende. (*Volcanic Islands*, p.42.)

Interestingly, Darwin did not draw any direct comparison between trachytes on the Azores and Ascension with those in Galápagos when he described the archipelago in Chapter V. In the subsequent chapter of *Volcanic Islands* (1844). Darwin published his theory on how basalts and trachytes might be related to one another by the 'sinking of crystals'. This was a novel theory at a time when most scientists believed that basalts and trachytes represented two distinct 'series' of igneous rocks that formed from different sources in the Earth. Darwin realized from his fieldwork on Isla Santiago, Ascension and Terceira, and reading the works of Beudant (1822), Scrope (1825) and Daubeny (1826), that trachytes frequently occur at the summit of volcanoes, which have also erupted basalt. He interpreted this close spatial association as evidence that the origin of basalt and trachyte was closely linked and in 1844 wrote:

> As the later eruptions, however, from most volcanic mountains, burst through their basal parts, owing to the increased height and weight of the internal column of molten rock, we see why, in most cases, only the lower flanks of the central, trachytic masses, are enveloped by basaltic streams. The separation of the ingredients of a mass of lava would, perhaps, sometimes take place within the body of a volcanic mountain, if lofty and of great dimensions, instead of within the underground focus; in which case, trachytic streams might be poured forth, almost contemporaneously, or at short recurrent intervals, from its summit, and basaltic streams from its base: this seems to have taken place at Teneriffe.* I need only further remark, that from violent disturbances the separation of the two series, even under otherwise favourable conditions, would naturally often be prevent-

> ed, and likewise their usual order of eruption be inverted. From the high degree of fluidity of most basaltic lavas, these perhaps, alone, would in many cases reach the surface. (*Volcanic Islands*, p. 121.)

Scrope (1825) had previously recognized the importance of density in controlling the compositions of volcanic rocks and stated that:

> Now the specific gravity of felspar is to that of augite, hornblende, and titaniferous iron, the other principal constituents of these rocks, in the average proportion of four to five. Consequently the specific gravity of a lava will vary directly with the proportion in which it contains the heavier minerals augite, hornblende, or titaniferous iron, which probably owe their superior weight to the quantity of iron that enters into their composition—and the two principal classes of lavas, the felspathic and ferruginous, producing severally on consolidation trachyte or basalt, might with propriety be distinguished as the *light* and the *heavier* lavas. (Scrope 1826:86.)

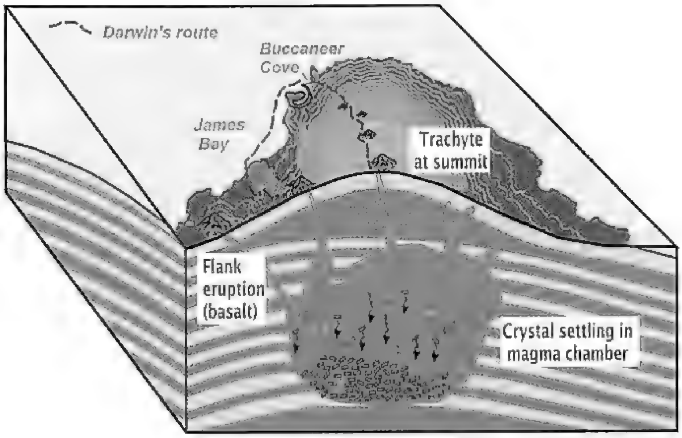

FIGURE 11. Schematic illustration summarising Darwin's ideas of how different types of volcanic rock may have formed and be related to one another on Isla Santiago (formerly known as James Island).

Nevertheless, unlike Scrope (1825), who advocated that trachyte was formed by melting granite, Darwin (1844) believed that basalt and trachyte formed by separation from a 'body of liquified volcanic rock' (p. 245; Table 1). Darwin proposed that the specific gravities of the crystallizing phases would lead to settling of phases heavier than the surrounding liquid, such as olivine, and form basalts whereas less dense phases (e.g., feldspar) would rise and form trachytes (Fig. 11). This theory was not widely accepted by scientists either at the time *Volcanic Islands* was published in 1844 or even in the following decades. Their ideas were in keeping with the later findings of the chemist Robert Bunsen (1811–1899) who in 1851 distinguished between volcanic rocks erupted from two different vents in Iceland, as a silica-rich 'acid' trachyte (rhyolite by today's nomenclature) and less siliceous 'basic' basalt[15]. Darwin's deteriorating health meant that he was not able to promote his ideas on the origins of trachyte and basalt and also it was at about this time that his studies moved away from geology towards his more famous work on the *Origin of Species*. As a result his ideas were not widely promoted and some scientists, such as Richthofen (1833–1905), continued to believe that basalts and trachytes were formed at separate periods of geological time (e.g., Richthofen, 1868). Others such as Scrope (1858) remained convinced that trachytes were formed by the melting of granite and had a separate origin to basalt. Over sixty years after the publication of *Volcanic Islands*, Harker (1909) high-

[15] In this article Bunsen included a discussion on the effects of gases in the formation of volcanic rock, based in part on his analysis of some of CD's specimens from the Cape Verde and Galápagos (palagonite tuff from Chatham Island). These specimens were sent by Darwin in 1847, *i.e.* after publication of *Volcanic Islands*. Shortly before sending the specimens Darwin had declared to Ernst Dieffenbach that 'I have for the present given up Geology, & am hard at work at pure Zoology'. See DarwinProject.ac.uk Letter 1569 — Darwin, C. R. to Kolbe, A. W. H., 5 May [1847]; Letter 1059 — Darwin, C. R. to Dieffenbach, Ernst, 9 Feb [1847].

lighted Darwin's idea that gravity settling of crystals from a basaltic magma may give rise to trachytes but this publication attracted little attention.

Conclusions

Whilst in Galápagos, Darwin used his keen collector's 'eye' to obtain a wide variety of igneous rocks. The most comprehensive set of volcanic rock types in his collection is from Isla Santiago (formerly known as James Island). Despite spending only ~three out of his ten days on the island collecting geological specimens, he managed to locate the full range of volcanic rock types that we now know constitute Isla Santiago. Darwin was interested in the processes involved in the diversity of volcanic rocks and whilst not specifically concerned with devising a scheme for the classification of volcanic rocks he did appreciate the importance of a common language for rock nomenclature. Both during and after the *Beagle* voyage, he was constantly revising his ideas on what types of volcanic rock he had observed and was clearly intrigued as to how best to account for their wide diversity. Darwin appears to have combined evidence from his blow pipe tests and mineralogical information in order to keep his volcanic rock nomenclature in line with current thinking. This revision of nomenclature was especially true of his specimens from Galápagos and led him finally to conclude in *Volcanic Islands* that most of them were basalts rather than trachytes as he had originally thought. Petrographic studies and new geochemical analyses have confirmed that Darwin did indeed only have one sample of trachyte from the archipelago. This was most likely collected from Isla Santiago, together with a trachyandesite, several large-feldspar basalts and olivine basalts.

Darwin inferred from his observations on the *Beagle* voyage and from reading the works of scientists such as Scrope (1825) and von Buch (1836) that trachyte and basalt were erupted more or less contemporaneously from the same volcano and that their compositional differences might be related by 'sinking of crystals' in a volcanic fluid (i.e., sub-volcanic magmachamber). His theory that basalts and trachytes might form from the same body of liquefied volcanic rock, by a process which is today commonly known as crystal settling, contrasted with the views of other scientists of the day who believed that trachytes and basalts were derived from different magmatic 'series'. If Darwin had realized that his collection of volcanic rocks consisted of specimens intermediate in composition between basalt and trachyte then he might have been able to strengthen his arguments for the existence of a continuum of magma types between basalt and trachyte. Darwin's ideas on sub-volcanic processes were largely overlooked until the end of the nineteenth century and he remains largely uncredited for his theory of crystal settling. The importance of this process was subsequently established by the classic experimental studies of N.L. Bowen (1887–1956) and is now fundamental to our understanding of the evolution and diversification of igneous rocks (Young 2002).

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Darwin, the Galápagos and his Changing Thoughts About Species Origins: 1835-1837

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Well before visiting the Galápagos Islands in September and October 1835, Darwin had embraced Lyell's teachings concerning the changes in land and sea and climate in past, present and future ages. He had also accepted Lyell's view that species extinctions and origins occur at all times. In February, 1835 he had broken with Lyell over the causes of some species extinctions. But he had had no reason to disagree with Lyell on species origins: any species is an independent creation with fixed characters, so there is no transmutation of species. The origin of any species occurs at just one place which is determined, and so explicable, by adaptational considerations alone. Darwin's Galápagos visit did not prompt any questioning of these Lyellian theses about species origins. However, less than a year later, in mid-1836, Darwin's discussions of the Galápagos mockingbirds, in his *Ornithological Notes*, show him to be now favoring transmutation, and to be finding support for this new view in the judgement that these birds differ varietally, but not specifically, on different islands. This new favoring of transmutation was not prompted by these reflections on these Galápagos facts, but by some other thoughts on some other facts. It is conjectured here that reflections, shortly before, on mainland South American bird biogeography, could well have occasioned this initial break with Lyell over species origins and prompted the shift to transmutationism. In early March 1837, several months after returning home to England, Darwin accepted John Gould's new judgements about his Galápagos bird specimens, and embraced two conclusions that he had never remotely contemplated before: namely, a general conclusion that many Galápagos landbird species, including the mockingbirds, were peculiar and so presumptively original to the archipelago while being very similar to other distinct species on the mainland; and a particular conclusion that the Galápagos mockingbirds comprised three distinct species, not mere varieties, peculiar to individual islands, and that they were distinct from all mainland mockingbird species. It was the novel general conclusion that convinced Darwin that his transmutationism was overwhelmingly vindicated. Within a few days, in his *Red Notebook*, he was integrating his disagreement with Lyell about species origins with his old disagreement over species extinctions. Within a few months, he was opening his *Notebook B* with a sketch of a comprehensive zoonomical system of theory conformed in its structure to the exposition given by Lyell of Lamarck's system.

1. Darwin in 1835: on the Extinctions and Origins of Species

By the time Darwin visited the Galápagos archipelago in September and October 1835, he had been committed for more than a year to Charles Lyell's views on the physical changes on the

earth's surface. There are aqueous and igneous causes for those changes in land and sea and climate taking place throughout the past, ever since the oldest known fossil-bearing rocks were laid down, and these causes continue in action at present and on into the future with the same kinds and sizes of effects. As for the coming and going of species, Lyell held, as no other geologist did, that the extinctions of species went on at all times in the past since the age of those strata, are going on now and on into times to come; and likewise with species origins.

The Darwin who was visiting the Galápagos had had no reason to disagree with these Lyellian teachings about species extinctions and origins. However, in February 1835, in his first overt break with Lyell concerning the living world, he had disagreed with his mentor about the causes of species extinctions. Lyell held that extinctions were caused by competitive upsets or defeating invasions brought on by changes in climatic and other local circumstances. Darwin, disagreeing, adopted a theory respectfully discussed but rejected by Lyell: the theory that species die because like any individual higher animal, and — as it was usually thought then — like a graft succession of apple trees, they have an intrinsically limited lifetime, an inherent mortality. So, on Darwin's new view — only given up entirely on reading Malthus in Autumn 1838 — failures to survive upsets or invasions may end some species lives before their limited lifetime has elapsed; but other species, in the absence of such circumstantial changes, have died from old age.[1]

This disagreement with Lyell over the causes of species extinctions obviously required no disagreement over species origins; and, indeed, on the origins of species, Darwin will make no break with Lyell until well after the Galápagos visit. Lyell did not claim to know what would be observed if naturalists were ever fortunate enough to witness a species originating. He did hold, however, that species are fixed in their characters, so that even in changing conditions in the long run they only diversify adaptively into intraspecific local varieties, never varying enough to give rise to new distinct species. In his terms, he opposed the transmutation of species. Accordingly, he opposed too what he called Lamarck's system, which he engaged as the most fully articulated system of transmutationist theorising. As an explicit alternative to Lamarck, Lyell took species to be special creations; each was a creation independent of any prior species. As a hypothesis, he assumed, further, that each species creation takes place at a single location, that there is a first pair of individuals or a lone hermaphrodite, and that the time and place of origin is providentially determined entirely adaptationally. The timing and placing are therefore explicable solely by adaptive considerations. The species originating at any location at any moment is the species best suited to the conditions there: physical conditions of soil, climate and so on, and other conditions arising from the plant and animal life already there. Lyell draws the most general biogeographical corollaries from this hypothesis: very different conditions in two regions will have called for the origins of very unlike species; while, if closely alike species, congeneric species, have originated in two areas that is because similar structure and functions have been required by similar conditions in those two places. The similarity among the species is due to, and explicable by, similarity in conditions where they originate.[2]

So, in sum, Lyell explicitly upheld five theses about any species origins: (i) independent creation (ii) fixity of character (iii) single original location (iv) one or two first individuals, and (v) adaptational determination of time and place. It is worth distinguishing these five theses because we can then understand how, in initially breaking with Lyell over the fifth, Darwin will be breaking with him too over all the others except the single original location thesis. Looking ahead, we shall see Darwin, in March 1837, five months after returning to England, recording in his *Red Notebook*, the earliest surviving theoretical reflections that show him to have disagreed decisively with Lyell in this way over the origins of species; and we shall see him integrating this break with the earlier one over the causes of species extinctions.

The question has to be posed then: how, when, and why had he first come to this change of mind over species origins? Was it very shortly before those notebook entries, and so well after his return to England, or was it many months earlier when still on the voyage, perhaps even as early as his visit to the Galápagos in 1835, and because of what he was observing, collecting and conjecturing there?

I shall be arguing that, on the most likely interpretations of all the documentary evidence that we have for his intellectual life over these two years, the change came neither when he was at the archipelago nor after his return to England. Let me emphasise right away that I shall argue that new reflections on the Galápagos bird species — reflections arising from John Gould's novel conclusions early in March 1837, about Darwin's Galápagos bird specimens — were overwhelmingly decisive for Darwin. For those reflections were decisive in convincing him that he was now unexpectedly and conclusively vindicated in his earlier tentative disagreement with Lyell's views on species origins, so that the time had now also come to act on that disagreement confidently and comprehensively. However, I shall be conjecturing that those March 1837 reflections — following the consultations with Gould — could be so decisive not because they were prompting that break for the first time; but, rather, because Darwin had already made that break, in mid-1836, a few months before the voyage's end in October, 1836; and I shall be conjecturing that at that time it was not reflections on any Galápagos observations or collections that were decisive in initiating this first movement away from his mentor's teachings on species origins.[3]

I should emphasise that the reconstruction given here of Darwin's changing thoughts over these two years is often complicated and sometimes conjectural. I shall ague that this is inevitable because no straightforward story sticking close to the texts is textually defensible. As happens often in biography, the textual evidence requires complications and conjectures if credible, coherent and encompassing interpretations are being sought. I should emphasise too, however, that in this Darwin case at least, the complications and conjectures are such that when we have worked our way through them they can be given succinct if not simple summaries; and that such succinctness is on offer at this paper's close; and I may note that it may be helpful for readers to allow themselves to go there — and to the paper's Abstract — right now, to get some sense of what conceptual and narrative issues have to be engaged next.

2. Darwin at the Galápagos and After

When at the Galápagos and shortly after, Darwin made extensive entries about the animals there in his *Zoology Notes*; and made comments too at that time in his *Field Notebooks*, in his correspondence and in his *Diary*. What none of these texts even hint at is that Darwin is being prompted to have any new thoughts about species origins by anything he has observed or been told. Hindsight may tempt us to read into some textual moments signs of some rethinking, but there is no ground for giving in to those temptations. To be sure, Darwin says of the lizards of the genus *Amblyrhyncus*: "I can not help suspecting that this genus, the species of which are so well adapted to their respective localities, is peculiar to this group of Isds". However, there is nothing in such a judgement that anyone who was in agreement with Lyell's views, as Darwin then was, would take as calling for any rethinking. A note records that Nicholas Lawson, the English Governor there, claimed to be able to tell with certainty from which island any tortoise had been brought. Again, on the mockingbirds, he writes: "This birds which is so closely allied to the Thenca of Chili (Callandra of B.Ayres) is singular from existing as varieties or distinct species in the different Isds." Noting that he has four specimens from four islands, he continues: "These will be found to be 2 or 3 varieties. Each variety is constant in its own Island … a parallel fact to the one mentioned

about the tortoises." But, once more, there is no sign here that these judgements, whether firm, tentative or vacillating, are being seen by Darwin as raising any issues bearing on any conventional or controversial positions on the origins of species.[4]

Quite generally, Darwin noted in his *Diary* when at the Galápagos: "It will be very interesting to find out from future comparison to what district or 'centre of creation' the organised beings of this archipelago must be attached." In his *Zoology Notes*, he is soon decided about the birds: "The Ornithology is manifestly American." He is unsure about the plants, noting in his Galápagos field notebook: "I certainly recognise S. America in ornithology, would a botanist?" Writing to John Henslow a few months later, he says that he will be curious to learn "whether the Flora belongs to America, or is peculiar." The contrast invoked in all such reflections and queries is the one familiar from the biogeography of the day, including Lyell's chapters. Animal or plant species peculiar to the Galápagos are those species thought to be living only on this land and so those species are presumed to have originated there. Darwin is judging that, unlike the lizards, the Galápagos birds include no peculiar species. The land birds evidently belong with mainland America as a center of species creations, as a site, that is, of species origins and dispersions; that is where these species are presumed to have originated, and so it is from there that individuals of these species are presumed to have migrated to the islands. For the rest of the voyage, Darwin will continue to presume that none of the Galápagos bird species is peculiar to the archipelago, and that all have originated elsewhere — in the case of the landbirds most likely in the Americas — before some individuals migrated to the archipelago. For the rest of the voyage, the presumptively-distant origins, American or otherwise, of the Galápagos bird species will have no bearing on any agreements or disagreements about species origins that Darwin is having with Lyell or any other mentor. The origin of the mockingbird species is no exception. Darwin presumes that this species originated on the American mainland. Only its Galápagos varieties will be judged to have originated on the islands; and it is only these island varieties that will be seen to have a bearing on species origins issues; and not until mid-1836, just a few months before the voyage's end in October 1836. The other Galápagos bird species will have none until early 1837, and so several months after he returns to England.[5]

Obviously, Darwin found the Galápagos archipelago instructive, dramatic and intriguing for all sorts of reasons: geological, botanical, zoological and so on. But there is just no call to interpret any of his responses to what he saw, heard about or collected on the islands when he was there as including, involving or implying fresh thoughts about species origins. Nor, as we move on through the next months through to mid-1836, is there any reason to think that the Galápagos — or any other region Darwin has visited before or after his time there — has occasioned such thoughts. For example, he certainly found the animals and plants of Australia and New Zealand curious in many ways; but there is no reason to interpret his reflections on them as signalling any new views about the origins of species. We may turn next then to famous entries made by Darwin in mid-1836, probably in June or July and so still a few months from landing back in England. They are entries within the pages he devotes to the birds of the Galápagos in his *Ornithological Notes*. These notes are not merely written out carefully; they are plainly composed by an author who knows where he is going, in moving from the opening of any line of reflection through its subsequent steps and on to its final conclusions.

The broad-ranging comments he makes about the islands and their animals and plants, in opening the section on the Galápagos birds, show no signs that he is linking any general judgements about this land and its inhabitants to any theoretical stances on species origins. Nor do the special remarks about the finches lead to any links. In numbers of species and individuals, they are the most abundant bird family, he says; but amongst these species there is, for him, "an inexplicable

confusion." There seems to be a gradation in the form of their bills; and he cannot distinguish the species by their habits, as they are all similar and feed together in large irregular flocks. By contrast, the particular notes devoted to the mockingbirds do end by making just such a link. Before the sentences leading to the making of that link, Darwin opens by reaffirming that these mockingbirds are very similar in appearance to the Chilean Thenca and Callandra of La Plata, and that in their habits he cannot "point out a single difference", although he imagined that their cry was rather different from the Chilean Thenca. He notes that he has specimens from the four largest islands, and that those from Chatham and Albermarle "appear to be the same; but the other two are different;" and he notes too: "In each Isld. Each kind is *exclusively* found; habits of all are indistinguishable." Then comes that linking:

> When I recollect, the fact that [from] the form of the body, shape of scales & general size, the Spaniards can at once pronounce, from which Island any Tortoise may have been brought. When I see these Islands in sight of each other, & [but *del.*] possessed of but a scanty stock of animals, tenanted by these birds, but slightly differing in structure & filling the same place in Nature, I must suspect they are only varieties. The only fact of a similar kind of which I am aware, is the constant asserted difference — between the wolf-like Fox of East &West Falkland Islds. — If there is the slightest foundation for these remarks the zoology of Archipelagoes — will be well worth examining; for such facts [would *inserted*] undermine the stability of Species.[6]

3. Mockingbird Varieties and Unstable Species

These cryptic sentences have attracted much attention over the years; and understandably so, as they are the only ones known from Darwin's voyage years where any explicit engagement is made with the issue of species transmutations. Rather surprisingly, perhaps, no one has analysed these sentences at length, phrase by phrase. I will be offering such an analysis shortly. However, before getting to the details it is worth standing back, and looking at the passage as someone might who has never met it before, someone who is considering the apparent drift of the passage as a whole. I would think that such a person might see three movements of thought here: first, a move from the particular case of the mockingbirds on separate islands to a generalisation about archipelagos having distinct varieties of species on separate islands; second, a move to the interest of archipelago zoology, and, third, a move to the undermining of the stability of species. What is more such a person would, I think, read these three moves as positive moves, that is as moves made by an author who is welcoming not resisting what comes at all the steps along the way: the case, the generalisation and its two corollaries, the interest in archipelagos and the instability of species. These are all welcome prospects. Indeed, given that this whole passage is evidently written by someone who has the ending in mind throughout, it would seem only right to suppose that all the moves made were designed to lead to the last as the final outcome. In sum, the Darwin who wrote this is here starting the work of making the generalisation well-founded because, if he can do so, he gets something from it that he wants — the undermining of species stability. What we shall see next is that a close scrutiny of the way the passage goes, phrase by phrase, confirms that this overall impression is correct. The passage is written by a Darwin who is glad to be marshalling this generalisation because he sees it as welcome support for unstable species.

In tracking what follows, it is crucial is to put out of mind any knowledge one may have about what is going to happen later, when Darwin has those new thoughts about the Galápagos birds following his new reflections on John Gould's new judgements about them in March 1837. For we need to avoid bringing to the reading of this passage preconceptions about Darwin's thinking that

are only appropriate to understanding how he is later going to be reasoning in March 1837. We need, rather, interpretative presuppositions appropriate to understanding him around June or July 1836.

More precisely, before undertaking a detailed exegesis, we should identify one particular mistaken preconception. In March 1837, it will be as judged by Gould to be not mere varieties but distinct species that Darwin will take the mockingbirds to be impressive evidence for transmutation. So, it is tempting to suppose that in mid-1836 it must also have been only as judged to be species not mere varieties that they could be thought by Darwin to support transmutation. However, we shall see shortly that, in mid-1836, it is exactly the other way round. Given the very different assumptions Darwin was then making about the islands and about these birds, it was only as varieties rather than species that they could have any bearing on the question of transmutation. At this time, if taken to be species they would have had, for Darwin, no bearing at all, much less any positive bearing, on the transmutation question. Why? Because in mid-1836 he is assuming that if they are species then they would have arrived on the Galápagos as three distinct migrant species that had originated on the continent of South America, perhaps on the nearest part and so on land he had not visited, the *Beagle* having sailed to the Galápagos by a north-westerly not a due westerly route. The contrast with March 1837 is then crucial. For it is from Gould that he will then learn what he had had previously no inkling of: namely, not only that they are species rather than mere varieties, but also that they are species not found on the continent and so are species that have presumably originated not on the continent but on the Galápagos .

We will be getting, in due course, to Darwin's new reflections in March 1837 on those new judgements by Gould. All one needs to grasp now is that Darwin's whole line of reasoning — in the mid-1836 mockingbird passage — is designed to decide between only two options; and that neither option involves any mockingbird species rather than varieties originating on the Galápagos. No such option is even in play implicitly. The reasoning only works as it does because that option is not in play. There is a varieties option and there is a species option, yes, but there is no option involving species that have originated on the islands. The species option assumes that any species now living on the islands would have originated on the mainland.

Consider next then the first conclusion Darwin reaches: that the mockingbirds differ only as varieties on different islands.A crucial point is that his use of the word "suspect" elsewhere shows that his use of that word here carries no implication of fear or distrust [7]. So, the conclusion may be rendered as saying that he must tentatively believe that the birds on the different islands are varieties. The tacit contrast is obviously with their being believed to be species.

He marshals five considerations as supporting this mockingbird varieties conclusion: 1. the tortoise report, 2. the closeness of the islands, 3. their scanty stock of mammals — in his voyage notebooks Darwin routinely uses this word "animals" to mean mammals, 4. the slightness of the mockingbird differences in structures, and 5. their filling the same place in the economy of nature — there are no differences, that is, in how they make a living, in where and what they eat and so on.

Let us take these considerations in turn. Strictly, the tortoise report implies one island only for each variety, and not one variety only for each island. But Darwin assumes both implications are true because he is asserting the parallel between the tortoises and the mockingbirds, and with the birds each kind is found exclusively on any one island even, as he notes, if one kind may be found on more than one island. These picky points are pertinent because, if two distinct kinds were to be found living on one island, their being distinct would suggest strongly that they were not interbreeding, which in turn would be grounds for judging them to be distinct species. So, in sum, the tortoise report supports the mockingbird varieties conclusion because of this parallel, with its

implication that there are no cases where tortoises or mockingbirds have more than one distinct kind on one island with no interbreeding.

The trick to understanding 2 and 3 is to see how they are complementary. The islands being so close as to be visible from one another is evidence that it is easy for plants and animals to migrate from one to another by flying, floating or whatever. By contrast, the scant stocking of the islands by land mammals shows how difficult it has long been for organisms of most kinds to migrate to the islands from the nearest mainland. Land mammals, as Lyell had emphasised and as Darwin had reflected before, are — precisely because of their poor powers of migration across ocean waters — good indicators of what changes in land and sea have or have not been going on over the eons in any region. For Darwin here, the scarcity of land mammals on the Galápagos shows not just the difficulty arising from the hundreds of miles of ocean now, but the unlikelihood of any complete or partial land bridge in the past. So, in sum, island to island migrations have been easy and frequent, mainland to island migrations very difficult and infrequent. Finally, 4 and 5 together emphasise that the structural differences, that allow Darwin to distinguish the kinds on separate islands, are not matched by any functional differences as they would be if these were distinct species.

As for the Falkland fox case, it is similar to the tortoise and mockingbird cases in that here too is an instance of this general fact: intra-specific, inter-varietal, intra-archipelago, inter-island differences. And that general fact is the decisive one for Darwin. Watch next to see how Darwin's argument for its instantiation by the mockingbirds invokes a contrast between two migration scenarios. What Darwin is arguing for is this: one migration from mainland to archipelago, followed by two or more migrations since from island to island with subsequent varietal divergences between mockingbirds on separate islands. What Darwin is arguing against is, therefore, a possible alternative migration scenario that he thinks is far less likely: three migrations of three species from the mainland with these three species landing up with only one species on any one island. The whole argument in favor of the varieties conclusion only works because the alternative, distinct species conclusion, requires the much less probable migration scenario. Notice, too, that the reasoning simply does not include, even as a possibility to be argued against, another, third migration scenario: namely, one mainland species migration to the archipelago with two or more island to island migrations followed by specific divergences on separate islands. This scenario is not in play, even tacitly, because Darwin is not even countenancing the possibility that there is any mockingbird species peculiar to the archipelago and presumed to have originated there. There is the variety judgement with its requisite migration scenario; and there is the species judgement with its very different migration scenario; and, because those are the only two options in the argument, any improbability established for the second option is so much probability conferred on the first. Some of the greater credibility of the variety judgement is independent of migration scenario considerations, but some is directly so dependent; and both lots of considerations favor the first judgement over the only alternative. It is on this view that there are only these two alternatives, and on this view that both lots of considerations must be figured in, and that the reasoning of the whole argument is grounded.

Turn now to the closing words. The inserted "would" does not complicate matters exegetically: it is simply required grammatically by the conditional, the "if". So, the last sentence is asserting that (if well- founded) the archipelago generalisation — about inter-island, inter-varietal differences — undermines species stability. Now, the parenthetic point about well-foundedness may be taken as given from here on, for obviously no ill-founded or unfounded generalisation could undermine anything of theoretical importance. As has been urged earlier, in this complex conditional sentence, if the generalisation has indeed any prospect of being well-founded, then archipelago zoology promises to be very interesting. So, the argumentational rather than presentational order is

from the generalisation to the species instability prospect, which prospect duly makes archipelago zoology of great interest.

Two questions now cry out for attention if this reading of this passage is even roughly right. Why did Darwin think the archipelago generalisation makes for species instability? And was he hopeful or fearful about this prospect? Take the second question, the attitude question, first.We have seen already that the structuring of the whole passage indicates a positive attitude. Darwin seems to be doing what comes before the punch line because he is wanting to secure that outcome rather than wanting to discredit it. Equally, the wording signals positive attitudes along the way: the conjunction of "slightest foundation" with "well worth" is surely hard to square with any suggestion that Darwin is stringing all these reasonings together because he wants to alert himself to a prospective path leading to an unwelcome destination. Let us stay, then, with the positive reading of this passage.

4 A Possible Inaugural Rationale for Favoring Species Transmutations

That other question can now be postponed no longer. If Darwin did think the archipelago generalisation — about inter-varietal, inter-island differences — undermined species stability, then why did he think this? The first and obvious point to make emphatically is that he would not have thought that this generalisation was inexplicable by anyone holding Lyell's views. This general fact was manifestly consistent with the view that species are fixed and vary only limitedly so as to diversify varietally but not specifically. Equally, then, he would not have been thinking such a generalisation required invoking any species transmutations for its explanation; these were not cases of specific transmutations, so they did not require explaining as the results of species transmutations. So, if they were not seen by Darwin as cases of transmutation, nor seen as requiring transmutations for their explanation, how could he think that they could contribute in any way to undermining species stability? A partial clue is in Lyell, where he reports Lamarck as supporting his case against the stability of species (Lyell uses this phrase) by citing the tendency of species to diversify into varieties on migrating to new areas with different conditions. But, as we have been insisting all along and as Darwin was fully aware, this tendency in species is one that Lyell's special-creation-of-fixed-species theses could easily accomodate. However, consider the mockingbirds as an instance of the archipelago generalisation: the varietal divergences have occurred following island to island migration; and, as Darwin plainly judged at this time, the islands did not differ in their conditions. So, I conjecture that this generalisation was thought by Darwin to bear on transmutation because adaptations to different conditions were not involved in these varietal divergences. The species had diversified varietally solely because of inter-island isolation. Why, then, was the generalisation decisive in making archipelago zoology bear positively, in Darwin's thinking, on the prospect of undermining species stability? Perhaps because, as a transmutationist, he could cite the generalisation as evidence that mere isolation, independent of any differences in conditions, suffices to cause varietal divergences that a transmutationist can interpret as the initial stages in species divergences. This conjecture about Darwin's thinking at this time may be supported by noting how he insists that, although distinguishably differing in structural characters, the mockingbird varieties are functionally the same, suggesting that the varieties are not adaptations to different conditions, but consequences of isolation alone as such, so suggesting that species may be made mutable by causes not taken fully into account by views such as Lyell's.[8]

We now can see where we have to go next. Darwin was favoring transmutation when in mid-1836 he writes this passage; but — as already emphasised — he would not have thought that these facts, these cases, or indeed the archipelago generalisation itself, required anyone, himself included, to give up special creations of fixed species; because these cases involve only inter-varietal not

inter-specific divergences, whether following mainland to island or island to island migrations. So, on the most probable reading of the famous passage from mid-1836, he must be read as someone who was not being moved to transmutation by reflecting on these archipelago facts, but as someone who was already favoring transmutation on account of other reflections on other facts; other facts which, unlike these, he would have taken to require transmutation for their explanation, other facts that he was judging to be not readily reconciled with Lyell's theses, other facts that he thought were most readily explicable as resulting from completed species transmutations. Now, this much is defensible on textual and contextual evidence alone. But plainly to accept this much is to face a further question, one which is beyond resolution on any direct documentary evidence.What other reflections on what other facts had prompted this inaugural favoring of species transmutations?

Faced with this question, we could go in at least three directions: (a) insist that this question is so difficult to answer that we should back up, reinterpret everything set out above, and find some other interpretative journey that avoids ever arriving at this question; (b) accept that we are faced with this question, but must reckon it unanswerable, and just proceed on to more answerable questions about what happens next to Darwin, especially when he gets back to England; or (c), finally, have a go at guessing, hoping though not expecting that one line of guessing may look more likely than others. Now, I know of no principles of proper procedure in doing the history of science that can dictate a choice among these three options. My training, my role models and my prejudices prompt a preference for the third, but my experience tells me that many other people are not like that. Readers who do not share my view in this matter may wish to skip the next few paragraphs and rejoin the story in the next section.

We want a guess that is guided by at least four desiderata: first, our guess should assume that Darwin had only recently — that is just before the mockingbird passage of mid-1836 — become inclined toward species transmutations for the first time; for, if he had long been favoring that view, we would probably find documentary signs of this inclination; second, our guess should take seriously the precise formulation of Lyell's alternative to species origins in species transmutations, and not represent Darwin as merely moving away from any old doctrine that we might call creationism; third, we need to find factual generalisations that Darwin is confident of at this time, in mid-1836, and which he will later argue are best explained by transmutation and difficult to reconcile with Lyellian special creations; fourth, we need a guess that coheres well with any reconstruction that we are going to give of what happens later, especially in March 1837, but not a guess that reads back uncritically issues that Darwin will only engage after his return to England.

On the guess that I favor, it is well worth looking at what Darwin has just been attending to, in mid-1836, in his *Ornithological Notes* almost immediately before the pages on the Galápagos birds. For he has just been discussing various genera of birds observed and collected much earlier on the voyage when he was on the mainland of southern South America. One genus, *Myothera* (later named *Pteroptochos* by Gould) can illustrate especially clearly what considerations about species origins may, just possibly, have been concerning Darwin at this time. This genus, Darwin emphasises, is peculiar to the most southern part of this continent, but within this broad area are found six distinct species often restricted to particular regions with very different conditions: arid or rainy or temperate. That much is explicitly noted in detail in his notes.[9] My guess is, then, that he could well have been interpreting these facts as anomalous for Lyell's view of species origins. For, at this time, Darwin's understanding of the history of that young land, fairly recently elevated above the sea, would have supported him in thinking that these species had originated pretty much where they now live, and that the conditions were then pretty much as they are now. So, on such a geologico-geographical interpretation, they could have been for Darwin cases of very similar species that have originated within one large area but in places within that area with very different

conditions. Their close similarities, close enough to make them congeneric species, cannot therefore be explained as required adaptationally by similar conditions because the conditions were not similar but different.

We need next to guess at what Darwin would have reflected if he had faced such a lack of explanatory fit between such facts and Lyell's theses about species origins. Well, let us recall how, in later years he would argue that, in any such cases, an explanation invoking common descent from a common ancestral species for all the species of the genus is a better explanation than any explanation ascribing the common characters to common adaptations to common conditions, because there were no such common conditions. This invocation of common ancestry for distinct congeneric species obviously requires inter-specific divergences from the one ancestral species, and divergences among the distinct descendent species, and so it requires inter-specific transmutations. This commitment to intra-generic, inter-specific transmutations must, therefore, replace any commitment to fixed, specially, separately, independently, created species. Indeed, after this shift to transmutation, all that would be left of Lyell's five theses would be the hypothesis of a single place of origin for each species.

It is worth dwelling on the reasoning posited by this guess about Darwin's first move to transmutations. This guess does not have him somehow witnessing new species arising from older ones. No, it has him moving to common intra-generic ancestry to explain facts that conflict with any common adaptation explanation for similarities among some congeneric species supposed to be special creations; and, it has him moving to transmutations, therefore, not initially because he wants divergences as causes of some otherwise-inexplicable inter-specific differences, but because he wants common ancestries as causes of some otherwise-inexplicable inter-specific resemblances. That one shift on that one issue brings with it an abandoning of all of Lyell's theses except one. Note too how the shift would have been understood by Darwin himself. As Lyell's discussion of Lamarck emphasised, the transmutationist position could be construed as taking the view Lyell held — of common descent within any species, and hence common ancestry as the cause of similarities among the varieties of that species — and doing what Lyell would not do: namely extrapolating that common ancestry, and so too that explanation for similarities among the descendents, to any genus comprising several similar species. For Lyell, conspecific varieties owe their common characters to their common ancestry, and owe their distinguishing characters to subsequent divergences. The transmutationist goes on to suppose that with more diversification there arise interspecific differences, and so a genus of distinct species owing their common characters to their common ancestry. And, again, as Lyell emphasised, this transmutationist need not stop extrapolating there, but can go on to wider and wider extrapolations, to families, classes and whole kingdoms, crediting shared characters to shared ancestry and peculiar ones to divergent descents — just as Lyell does intraspecifically and intervarietally, but only so.

These points all bear directly on what further guesses we should be making about the relations between two clusters of issues engaged by Darwin at this time, if our guessing is roughly right so far. If it was the *Myothera* facts, or others like them, that were the first to be explained by him as cases of completed species transmutations, then we may say that this shift to this explanation was Darwin's initial and primary rationale for first favoring transmutation as such. What then of the intervarietal divergences among the Galápagos mockingbirds? These would have been entering into his new transmutationist thinking in quite another way; not evidencing transmutation as such because not requiring explanation as cases of completed transmutations. No, they are cases of incipient species transmutations that have only gone as far as intervarietal divergence. And so it is not this intervarietal divergence by itself that is decisive; it is the circumstances of it: on islands that are the same in conditions and among varieties filling the same places in the economy of

nature, suggesting that mere isolation itself is making these species unstable. At this stage then, if all this guessing is not hopelessly wrong, the mainland bird genera and the archipelago bird varieties are making quite different contributions to Darwin's new transmutationist thinking about species origins. Moreover, on this guess, the mainland reflections, about such genera as *Myothera*, have priority; while the island reflections are supplementary in bearing, not on the primary issue of the explanatory need for transmutation itself, but on the secondary issue about what circumstances may be effective in starting transmutations. We need, then, to distinguish from now on between that earliest, primary rationale and this subsequent, secondary, supplementary one.

Mid-1836 to March 1837 is well over half a year, and it may seem odd to skim over that whole period here. But we do so for good reason: although studied closely, the documents from those months have never been found to include any indications of any further developments in Darwin's views on species origins. The supposition, the guess, made here is, therefore, that Darwin continued inclining toward transmutation and continued his commitment to the primary and secondary rationales for transmutation without any experiences or speculations prompting him to develop that thinking beyond where he had gone with it in mid-1836. One further guess would naturally credit him with holding these transmutationist views only tentatively, very mindful as to how controversial they would be and so how fitting it could be to put off exploring all their implications until other, more pressing duties were discharged both while at sea and back in England. In any case, we here must proceed on the assumption that in early 1837 — when he begins learning of Gould's judgements on his specimens — his thinking was still pretty much as set out in our distinguishing of the primary and the secondary rationales for his mid-1836 transmutationist views.

5. The Gould Consultations and After

This distinction between the two rationales can throw light on why Darwin was so massively impressed by the new judgements that Gould would make about the Galápagos bird specimens. Those judgements transformed the Galápagos in two ways. First, they changed the Galápagos islands from being the site for a secondary, supplementary rationale for transmutationism, to becoming a stellar instance of the primary rationale: distinct species originating in locations with very different conditions, the arid islands and the lush nearest mainland. Second, they enhanced the secondary rationale by raising the mockingbirds from varieties to species, species moreover original to their islands, not to the mainland where, Gould insisted, those species were unknown.

There seems to have been a crucial meeting with Gould at the Zoological Society within three or four days of Darwin moving to live in London on March 6.[10] On a single sheet of paper, Darwin noted down what were for him the decisive details about the landbird species collected from the Galápagos. The principal exercise was simple enough: to list all the landbirds in no special order, to note if they were peculiar to the archipelago, and to note if they belonged to genera peculiar to the Americas. The results from the exercise would be summed up by Darwin within a month or two when composing the Galápagos chapter of his *Journal of Researches* published two years later. After discounting various exceptional and uncertain cases, Darwin had some ten species, including a buzzard species, the three mockingbird species, a species of dove, a species of swallow and four other species supporting the general claim that, among the landbirds, many were species peculiar to the archipelago but exclusively American in general structure, habits, coloring and cries.[11]

We can see now why we have to distinguish in this way between two main conclusions that Gould's judgements enabled Darwin to reach about the Galápagos bird specimens: a general conclusion covering several species, including the mockingbirds, and a particular judgement about the

mockingbirds alone. The general conclusion was the influential one concerning Darwin's transmutationist convictions at this time. For Darwin, this generalisation suggested a completely novel geologico-geographical reflection: many landbird species had originated on those young arid volcanic islands and yet were very similar to species that had already originated in very different conditions on the nearest older continental land, rather than resembling the species that had originated on other arid, volcanic oceanic islands elsewhere in the world. These similarities are then explicable not as common adaptations but rather as due to common ancestries. This reflection was exactly in accord with what we have distinguished here as the primary rationale for Darwin's transmutationism. Note, too, that it is Darwin's engagement with Lyell's geologico-geographical theorising that takes him far beyond where Gould's judgements went in themselves; and that the influence on Darwin of this general conclusion about the Galápagos landbirds does not depend on that land being so many islands. This generalisation would have been no less massively influential for Darwin's transmutationist convictions if that land had comprised only a single oceanic island.

Consider next what is now new in Darwin's special reflections on the mockingbirds. Their specific divergences have arisen not just between Galápagos descendents and mainland ancestors, but also following later migrations from one island to another. Here, with the mockingbirds, it is crucial that the Galápagos land is a cluster of islands. Notice, however, that this special conclusion about these birds bears on the secondary rationale — isolation as conducive to transmutations even with no differences in conditions — not on the primary rationale. This point is well worth clarifying because one often reads biographers of Darwin, knowledgeable specialists some of them, saying in effect that it was above all, or even solely, the Galápagos mockingbirds, just these three species, that somehow sufficed to move Darwin, as the usual phrasing has it, from creation to evolution. Any such claim is narratively misleading because analytically too indiscriminate. Along with other species, the mockingbirds — on the mainland and the islands — came within the general conclusion bearing on the primary rationale. On their own, the three archipelago species also bore on the secondary rationale. The primary rationale concerned common ancestry as causing resemblances among species originating in different — mainland and island — conditions; the particular conclusion about those three island mockingbird species concerned isolation as causing differences between species originating on islands with apparently the same conditions. So, the mockingbirds were special in uniquely contributing to both rationales; but, they contributed most decisively, along with other species, through the primary rationale.

In the early months of 1837, Darwin was reflecting also on new judgements made by Richard Owen about his South American fossil mammal specimens. These new judgements confirmed for Darwin a generalisation he had long embraced and which he knew Lyell had too: the law of the succession of types, the law that the extinct species found as fossils in any area of land today are often of the same genera or families as the extant species living there now. In itself that generalisation would not have led Darwin to any disagreements with Lyell, nor therefore led him to incline to transmutation for the very first time. However, one new example of it does feature in his *Red Notebook* theorising in early March 1837. Bones Darwin had thought might be remains of an extinct mastodon species were interpreted very differently by Owen, so that Darwin was soon thinking of this species as a large extinct llama species like those species of smaller llamas living in South America. He went on to draw a parallel, between the relationship between these species over time, and the spatial succession shown by two living species of *Rhea* (or ostrich) species, the larger northern species and a smaller congener to the south; and he speculated that in such cases, where the two species overlapped in range, the transmutation would have been saltationary not gradual.[12]

At the same time, in this notebook, Darwin draws another parallel, between what determines

the timing of species extinctions and what determines the placing of species origins. Some groups of species, among the mammals especially, have not had any of their species originate in some areas where they flourish once they get there with man's aid. This flourishing shows that those original absences cannot be explained as due to lack of adaptation of that group to the conditions there. Hence, for Darwin, the parallel with species that have died from old age in unchanging conditions, and not because they failed to adapt to any changes in conditions. The implicit reasons for this parallel were assumptions about limited ancestral inheritances. The regional absences are due to all the species in the group descending from one ancestral species none of whose descendents has succeeded, before man helped, in migrating to those regions. The origins of species of that group are regionally limited because of ancestral and migrationary limitations, not because of adaptive unsuitability. Likewise with some species extinctions; these are due to the propagation, within any one species, of a durationally limited species life from the earliest to all later members, with the species extinction eventually coming not from adaptive failure but from the ending of that transmitted, limited duration.[13]

It was Lyell who had taught Darwin to consider parallels between temporal, geological successions and spatial, geographical ones. But here, obviously, Darwin is disagreeing with Lyell over the assumptions to be brought to the explaining of any parallels. For Lyell, it is adaptational considerations alone that determine and so can explain the timing and placing of the coming and going of species. For Darwin, species are exquisitely adapted to their habitations (areas, ranges), stations (habitats) and places in the economy of nature (niches), but he held that adaptational considerations alone do not suffice explanatorily. They must be augmented by supraspecific ancestral and migrational considerations. Such considerations had a place already in Lyell's historical geography for individual species: any Old World species, say, that has flourished in the New World, once taken there recently by man, owes its earlier absence there to its having originated in one place in the Old World and its failure to migrate there unaided. With common ancestry extended to supraspecific groups, Darwin could, in March 1837, explain the absence of whole groups from areas where they could flourish once aided in getting there. It had been, I have guessed, another, earlier geologico-geographical explanatory need for extended, supraspecific common-ancestral considerations that had first inclined Darwin to become a transmutationist in mid -1836; and it is thanks to these new developments of these further needs that his transmutationist convictions are being strengthened so hugely, so unexpectedly, so irreversibly and so consequentially in March 1837.

Lyell had said that anyone considering adopting the transmutation of species would have to confront too all the other theses — continued spontaneous generations of the simplest organisms, escalation over eons from those simplest ones to the highest animals and an ape ancestry for man — all elaborated in what he called Lamarck's system. Lyell meant this point to serve as a warning; but Darwin evidently took it as a challenge from which a grandson of Erasmus Darwin should not shrink. By July 1837, at the opening of his *Notebook B*, he had duly taken the most consequential intellectual decision of his life so far: to elaborate a system of zoonomical theory with the scope and structure of Lyell's version of Lamarck's system. Under the heading *Zoonomia*, the laws of life — the title of his grandfather's best-known work — the first two dozen pages of Charles Darwin's *Notebook B* sketch such a system. All sorts of reflections about all sorts of Galápagos plants and animals now enter in all sorts of ways into that sketch. But that is another story for another time. What needs insisting on here is that although Darwin's implementation of that decision went far beyond any theorising prompted by the Galápagos material alone, the decision itself had been taken directly in the wake of those new interpretations of the archipelago's landbirds prompted by the new judgements communicated by Gould to Darwin in March.[14]

6. Concluding Remarks

It has been argued throughout this paper that any account of Darwin's changing thoughts about species origins — from his first visiting at the Galápagos islands themselves to his rethinkings in March 1837 — has to be analytically and narratively complicated. It will also now be clear that the account given here is indebted at every turn to the researches of Frank Sulloway. However, my conclusions are at odds with those he first reached some decades back and which have been justly admired and widely accepted as authoritative since. The central thesis in Sulloway's account is that, over these two years, Darwin's attitude — positive or negative — towards species transmutation was always correlated with, if not solely conditioned by, his response to a single question about one lot of birds, the Galápagos mockingbirds: are they species or varieties? Accordingly, Sulloway has Darwin in October 1835, at the time of the Galápagos visit, vacillating about that question — species or varieties — about those birds, and therefore vacillating about accepting or rejecting transmutation; while in mid-1836, Sulloway has Darwin deciding for varieties and against species, and so deciding against transmutation; then, finally, with Gould's judgements accepted, Sulloway has Darwin reversing his mind on both questions in going for species and so for transmutations. Now, if the present paper is anywhere close to being analytically and narratively on target, no such scheme as Sulloway's can be accepted; for it does not take adequately into account the decisive changes in the assumptions Darwin was bringing to his engagement with these issues: most crucially, the change from assuming — from October, 1835 to March 1837, and so in mid-1836 — that, if the mockingbirds were distinct species from one island to another, then they were species original to the mainland not to the archipelago, to assuming, after Gould's input, that they were indeed distinct species and moreover different from any on the mainland and so original to the Galápagos.[15]

As for my account, it has some straightforward moments that may be worth recalling here. For more than a year before the Galápagos visit in September and October 1835, Darwin had embraced Lyell's geological views and had had no disagreements with Lyell's special creationism concerning species, nor then with Lyell's rejection of species transmutations. Moreover, Darwin had no such disagreements when at the archipelago. By contrast, if we fast forward to March 1837, several months after his return to England, Darwin is showing himself to be now a completely and confidently convinced transmutationist in his *Red Notebook*. The interaction with John Gould concerning the Galápagos birds has contributed decisively to this new complete confidence. Next, sometime between early March and his opening of his *Notebook B* in July, Darwin took the most consequential intellectual decision of his entire life: he would side with Lamarck rather than Lyell on the organic world, and work at elaborating a system of theory with the scope and structure of Lyell's version of Lamarck's system.

So far so straightforward, at least in recapitulationary outline. But what about those months between visiting the Galápagos and interacting with Gould? What about Darwin's engaging with the issue of species transmutation in his reflections on the Galápagos mockingbirds in his *Ornithological Notes* in mid-1836? I have concluded that he was already favoring transmutations before recording those reflections, and was then looking to some prospective support for that view from archipelago zoology. But why was he already a transmutationist at that time? I argue that his first shift to favoring transmutation had most likely already been made shortly before; but that it would not have been prompted by any thoughts he was then having about the Galápagos birds. We will probably never know what other reflections on what other facts had prompted that shift. My guess is that the decisive new reflections did not concern any islands; rather these new thoughts may have concerned the geographical distribution of some genera of birds observed and collected by Darwin

years earlier, on the mainland of southern South America. So, my guess is that it was reflections on these genera, reflections first made in mid-1836 just before the mockingbird entries in the *Ornithological Notes*. This guess is only a guess but it could help explain why Gould's later judgements on the Galápagos bird specimens were so massively influential. Gould's judgements — quite unexpectedly for Darwin — meant that these archipelago birds now raised the same issue about the origins of species that had been raised for Darwin, according to my guess, by those mainland genera: the issue of why very similar species had originated in places with very dissimilar conditions.

Finally, what of Darwin's own recollections of his changing thoughts about species origins during and after the voyage? The pertinent passages in the *Autobiography*, in the *Origin* and in *Variation under Domestication*, and similar passages in letters, are now well-known to project back, into the voyage years, judgements and inferences not made until after Darwin got back to England. So, these passages can make no contribution to any historians' quests for biographical alternatives to anachronistic retrospections. Darwin wrote late in life to a German correspondent, who had asked about the early development of his thinking, that when on the *Beagle* he "believed in the permanence of species, but, as far as I can remember, vague doubts flitted across my mind." In its own vagueness this memory is consistent with the analysis given here. Much earlier, in 1844, he told his friend Leonard Jenyns that he had first approached the subject of species mutability not from "the difficulty in determining what are species & what are varieties" but, rather, "from such facts, as the relationship between the living & extinct mammifers in S.America, & between those living on the continent & on adjoining islands, such as the Galápagos." This account plainly recalls early March, 1837, rather than any voyage moments, as it emphasises resemblances between mainland and island species rather than differences among island species or varieties. Even earlier, in his own personal journal, writing most likely in August 1838, he explicitly recalled opening his *Notebook B* in July 1837 — what he identified here as "my first note Book on 'transmutation of species' " — after having been "greatly struck" from "about … March" that year "on character of S. American fossils — & species on Galápagos Archipelago." He continued: "These facts origin (especially latter) of all my views." Again, this phrasing indicates a recollection of being most impressed not just with Gould's mockingbird judgements in particular, but with the generalisation drawn from many instances, including the mockingbirds, concerning resemblances among distinct species on the mainland and on the islands.[16]

If we look back and ask ourselves what do these recollections leave out that we have had to include, one short answer is inevitable because it leads to so many indispensable complications and conjectures. That short answer is, obviously, Lyell's views. That short answer is an obvious answer but not a superficial one, if only because it is grounded in an observation familiar to all who have concerned themselves with the intellectual lives of scientific theorists: such theorists, even — perhaps especially — the very innovative ones, often make up their minds about the way the world goes by working out how far they can agree, and how far they must disagree with views already put in play by others. The parallel is absurdly hubristic, but if this paper is at all successful then its complicating and conjectural proposals about Darwin will provoke rewarding agreements and disagreements for some Darwin buffs to engage as they recover from their bicentennial fatigue.

Acknowledgements and a Bibliographical Note

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ent paper supplements two earlier ones of mine often travelling over the same ground, Hodge 1982 and 1990.The second of these papers corrects consequential mistakes made in the first, including mistakes about Darwin's mid-1836 views about the mockingbirds, errors pointed out by Sulloway's publications at that time. This second paper defends most of the main views I have argued for here, while explaining more fully my agreements and disagreements with Sulloway's conclusions. These papers also document more precisely my debts to Ghiselin, Herbert and Kohn. Both papers, reprinted in facsimile in a volume published recently, Hodge 2009a, develop extensively the theme that has had to preoccupy this paper: how Darwin in 1835-7 was often working out his thoughts about what he found in the world by reflecting on his agreements and disagreements with what he found in Lyell's *Principles of Geology* [17].

Most of Darwin's writings from the 1830s, including notebooks that are still unpublished in printed editions — often together with transcriptions and editorial and bibliographical commentary — are now available at the invaluable website directed by John van Wyhe: *The Complete Work of Charles Darwin Online* (darwinonline.org.uk/).

End Notes

1. Hodge 1982 and 1990. Everything said here about Lyell's views is documented in the first of these papers. On Darwin and Lyell's geology, see now Herbert 2005. For comprehensive and detailed accounts of Darwin and the Galápagos, see Sulloway 1984, Darwin 2009 and Grant and Estes 2009. For a concise, general account of Darwin's thinking before and during the voyage years, see Sloan 2009.
2. Hodge 1982:6–13 and 28–35.
3. Hodge 1990.
4. *Zoology Notes*, MS pp. 340, 328 and 341, in Darwin 2000:296, 291 and 298.
5. Darwin 1989:356; *Zoology Notes*, MS p.340, in Darwin 2000:297; *Galapagos field notebook* MS p. 30b, in Darwin 2009:439; Darwin 1985:485. On all of Darwin's diaries, journals, notebooks, specimen catalogues and other records from the voyage years, see the editors' account in Darwin 1985:545–548.
6. *Ornithological Notes*, MS pp.71–4, in Darwin 1963:261–2. For the dating of these notes, see Sulloway 1982b:327–337; for Darwin's changing views on the finches, see Sulloway 1982a.
7. Hodge 1990:273; Sulloway 2009:23–24. Here, I am agreeing with Sulloway in disagreeing with Kohn et al. 2005.
8. See Chancellor and van Wyhe's commentary in Darwin 2009:410.
9. *Ornithological Notes*, MS pp. 64–9, in Darwin 1963:255–259. Some birds of this genus were called Antbirds. For detailed discussion of them, see Herbert's notes in Darwin 1981:111–115 and Sulloway 1982b:374.
10. For full documentation and extensive analysis, see Sulloway 1982b:362–374.
11. Darwin 1839:461–462. For a detailed account, see Sulloway 1982b:362–374.
12. *Red Notebook*, MS pp. 127 and 130, in Darwin 1987a:61–63. For the dating of these entries see, Darwin 1981, Sulloway 1982b and 1983, and Darwin 1987a. For Darwin's consultations with Owen, see Brinkman 2010. This very informative paper suggests that while still on his voyage Darwin inclined toward species transmutations on paleontological grounds. I am unpersuaded and would stand by what I said about Darwin's paleontology in Hodge 1982, an account not discussed by Brinkman.
13. *Red Notebook*, MS p. 133, in Darwin 1987a:63. Details in Hodge 1982:43–50.
14. Hodge 1982, 1990 and 2009d.
15. Sulloway 2009 reaffirms the views set out in Sulloway 1982b, but without referring to the agreements and disagreements with those views in Hodge 1990.
16. See volume one of Darwin 1903:367; Darwin 1987b:85, and Darwin 1986:431.
17. Likewise for the early Wallace too: a main challenge came in disagreeing with and replacing Lyell's view that, on a neoHutonian earth's surface, adaptation alone determines the timing and placing of the continual origins and extinctions of species, and so — together with constantly changing avenues and barriers

to migrations — determines the temporal and spatial representations of supraspecific groups. For detailed comparisons of Darwin and Wallace on this very general issue, see Hodge 1991; for a brief introduction, see Hodge 2009b and c.

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Going Public on the Galápagos: Reading Darwin Between the Lines

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Darwin became an evolutionist soon after his return from the voyage of the *Beagle*. In early publications he provided material the evolutionary significance of which only became explicit in his later ones. Passages in the *Journal of Researches* are particularly interesting, especially with respect to the Galápagos, because there were two editions. Darwin enlisted the aid of specialists in getting his materials worked up, but keeping his theories to himself made it difficult to get the sort of treatment that he needed. Editing the *Zoology* of the voyage was part of that effort, and the volume on birds contains major input from him. Darwin's monograph on the Cirripedia (together with its appendices of the fossil cirripedes) was his first book on evolution. He resorted to explaining his evolutionary ideas to his confidants Joseph Dalton Hooker and Asa Gray. Wallace was able to take hints that Darwin provided in the *Journal of Researches* and create his own version of the theory.

It is difficult to read Darwin's *Journal of Researches* oblivious to the fact that Darwin was also the author of *The Origin of Species*. Naive reading of the *Journal* must have contributed to popular misconceptions of his career, including the myth of his having become an evolutionist during his encounter with the biota of the Galápagos Archipelago (Sulloway 1982; Hodge, this volume). There is compelling evidence that Darwin did not become an evolutionist until after his return to England. Hints about evolution and natural selection were added to the *Diary* upon which the first and then the second editions were based (Keyes 1988; Darwin 1839, 1845). Nonetheless these documents provide valuable clues that allow us to reconstruct the history of his intellectual development.

If Darwin was not discovering evolution during his visit to the Galápagos, what was he doing? The most obvious and straight-forward answer is geology. Interested in geology from the outset of the voyage, he was profoundly influenced by Lyell's *Principles* (1830–1833) and the subject soon became his main focus of research. His geological research was guided by his development of important hypotheses including his view of uplift and subsidence on a vast scale. That line of reasoning led him to develop his theory of coral reefs, while he was still in South America. His geological work in the Galápagos was part of the same research program, and he presented it as such. But of course throughout the voyage Darwin was collecting extant plants and animals, and studying their geographical distribution and autecology. We know from his correspondence that he intended to consider the biota of the archipelago from the point of view of "centers of creation." Although it is problematic whether Darwin had an "invertebrate program" while on the *Beagle*, he definitely intended to study marine invertebrates, especially ones that were poorly known. His work on chaetognaths is a particularly good example (Darwin 1844). His zoological observations

were often focused upon animals that seemed rather anomalous from the point of view of their behavior. These include woodpeckers that never climb trees, and various primarily marine animals with terrestrial representatives. Early in the voyage he was fascinated by terrestrial flatworms, later on by terrestrial crabs. True to form, while in the Galápagos Darwin paid special attention to the marine iguanas and compared them to the terrestrial ones. One thing that interested him about the birds was that they were so tame. During the voyage Darwin believed that there could be adaptive modifications within species, and behavior was an important component of such adaptation. Turning that belief into a truly evolutionary view of things was a later development, but he made it implicit in the *Journal of Researches*.

Tradition has it that Darwin kept his evolutionary ideas almost entirely to himself. His notebooks have to be read as "private dialogue" in the strictest sense. But he did confide in certain of his friends and professional colleagues, most notably the botanist Joseph Dalton Hooker. They discussed evolution and natural selection in correspondence, and one wonders what went on in conversation. One also wonders what Darwin's contemporary readers might have made of the implicitly evolutionary passages in his earlier publications that became explicit evidence in his later ones. For example, in the *Journal of Researches* Darwin alludes to Robert Malthus's ideas about population. He writes: "The supply of food, on an average, remains constant; yet the tendency in every animal to increase by propagation is geometrical; and its surprising effects have nowhere been more astonishingly shown, than in the case of the European animals run wild during the last few centuries in America." (Darwin 1845:175.) One also might wonder what an evolutionist such as Alfred Russel Wallace would have made of that, and just how "independent" the discovery of natural selection by the two of them really was.

With the passage of time Darwin's remarks about matters of evolutionary interest became increasingly explicit. The habits of the tucutuco (*Ctenomys brasiliensis*), a blind, subterranean rodent convergent with moles, are discussed in some detail in the first edition of the *Journal of Researches* (Darwin 1839:58–60). In the second edition he considers how Lamarck would have explained the gradual rudimentation of the eyes via intermediate forms (Darwin 1845:52).

Perhaps the most significant of Darwin's cryptic remarks about evolution occurs in the second edition of the *Journal of Researches*. It is about the Galápagos finches and is particularly important because Wallace refers to it. Darwin (1845:380) writes: "Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends."

And then there is a passage on the barnacle *Pollicipes* in the *Fossil Lepadidae*. Darwin (1851:48) writes: "This, the most ancient genus of the Lepadidae, seems also to be the stem of the genealogical tree; for Pollicipes leads, with hardly a break, by some of its species into *Scalpellum villosum*; and Scalpellum leads by Oxynaspis into Lepas and the allied genera: *Pollicipes mitella*, moreover is nearer allied to the Sessile Cirripedes than is any other Pedunculated cirripede, except, perhaps, Lithotrya, which is also closely connected with Pollicipes." Although this passage might be interpreted metaphorically, it is obviously about common ancestors and branching sequences.

Before addressing the question of why Darwin made such remarks, especially the one about the Galápagos finches, we should make sure that we understand the kind of biogeography that Darwin aimed to replace. Charles Lyell, in his *Principles of Geology*, had presented a kind of equilibrium theory. Unlike Lamarck, Lyell believed in extinction. He also thought that new species must come into existence, preserving the balance. They would originate in a particular place (center of creation) and then migrate elsewhere (rather like animals from Noah's Ark). What "struck" Darwin upon his return to England was the point that the mockingbirds were closely related, suggesting

that in addition to moving from one place to another, groups of organisms would, as we now put it, speciate. Such speciation must be kept conceptually distinct from mere modification as invoked by Lamarck and others: the species split into separate lineages that diverge, and split and diverge again. It was also quite different from the kind of diversification *within* species that was familiar to naturalists. (see Hodge, this volume.)

Returning to the pre-*Origin* adumbrations of evolutionary biology, there are some very straightforward reasons for Darwin's not keeping everything to himself. Evolution had become for him a major research program, one to be expanded and developed once he got his major geological contributions published. He needed data, including data based upon his own collections. But he wanted data that would bear upon his hypotheses, and that sometimes posed a problem. Other scientists were not necessarily asking the kinds of questions that he hoped to get answered. The evolutionary materials presented in the *Journal of Researches* would provide something of a preliminary statement of his findings. On the one hand he could, and did, cite them in his explicitly evolutionary works. On the other hand, drawing attention to phenomena of evolutionary interest might encourage further research along such lines.

Darwin sent out a questionnaire about domesticated animals and plants. He was also appointed to a committee of the British Association for the Advancement of Science to design a questionnaire about human races. The choice of him as a member is not particularly problematic. He was on the scene at the Birmingham meeting in August of 1839, and his *Journal of Researches* had been published on June 1 of that year. Therefore he was well known as a scientific traveler, and had desirable experience as well as relevant interests. Another committee to which he was appointed, on zoological nomenclature, was established on February 11, 1842. It produced the Strickland Code, which evolved into our modern International Code of Zoological Nomenclature. Drafts of the code were circulated to various zoologists for their advice. The membership of the original committee was as follows:

Mr. C. Darwin
Prof. Henslow
Rev. L. Jenyns
Mr. W. Ogilby
Mr. J. Phillips
Dr. John Richardson
Mr. H.E. Strickland (reporter)
Mr. J.O. Westwood

Added later:
William John Broderip
Professor Richard Owen
G.R. Waterhouse
William Yarrell

We should not make too much about it, but several of these people were involved in working up Darwin's collections for him. One of these was John Stevens Henslow (1796–1861), Darwin's teacher at Cambridge, who had cared for the collections in Darwin's absence. Darwin was awarded a grant from the Admiralty to publish the *Zoology* of the Voyage (1839–1843). Leonard Jenyns (1800–1893) did the section on fishes. George Robert Waterhouse (1810–1888) did the section on mammals, and Richard Owen (1804–1892) that on fossil mammals. All three of them had important discussions with Darwin about the fundamental principles of systematics. At that time, Darwin had not yet done any systematic work himself, although he intended to describe some marine animals. He needed to get specialists to work up the materials for him and, he hoped, to include the kind of information that he needed for his own work. As editor, Darwin had some control over what went into the reports. He added a lot of material on behavior and geographical distribution based on his observations in the field. The section in which he took the most active editorial part was that on birds. These had been turned over to John Gould (1804–1881), who had done the initial descriptions of the birds that played such an important role in making Darwin an evolutionist. Gould departed for Australia on May 16, 1838. In 1840, George Robert Gray (1808–1872) helped to com-

plete the manuscript and check the proofs. There was also an anatomical appendix by Thomas Campbell Eyton (1809–1880). Darwin and Eyton had been friends as undergraduates at Cambridge. Eyton later provided Darwin with material on the variability of domesticated animals.

FIGURE 1. (A) Henry Walter Bates, 1825–1892, (B) Edward Blyth, 1810–1873, (C) Thomas Campbell Eyton, 1809–1880, (D) William Darwin Fox, 1805–1880, (E) John Gould, 1804–1881, and (F) Asa Gray, 1810–1888.

In addition to the living mammals of the voyage, Waterhouse described many of the insects, including some Galápagos Coleoptera (Waterhouse 1845). In 1845, Darwin and Waterhouse exchanged many letters about the biogeography of the Galápagos Coleoptera. Some new material was available just in time for Darwin to use it in the revised edition of the *Journal of Researches*. A letter from Waterhouse to Darwin in June, 1845, with an extract from his paper in the *Annals and Magazine of Natural History* (Waterhouse 1845) Waterhouse says that he found no species in common from different islands where locality data were provided. Another letter from Waterhouse to Darwin, dated July 11, 1845, based upon more specimens of Galápagos Coleoptera, again observes that no species were common to two islands (Darwin 1845:395). Waterhouse obviously provided this kind of information at Darwin's urging.

Waterhouse shared Darwin's interest in geographical distribution and the principles of classification. Their interaction reveals much about how Darwin exchanged ideas with his colleagues. Their correspondence on the principles of classification began on July 26, 1843. In January of 1847, Darwin's review of a book on Mammals by Waterhouse was published. On October 1of the previous year, Darwin had begun to work on barnacles. One thing led to another, and the result was a huge monograph, with two volumes devoted to the living cirripedes and the parts on fossil forms published separately, making it appear that it was several monographs instead of a single work.

The comparative anatomist Richard Owen described the fossil mammals. The close relationship between extant mammals and extinct ones was one of Darwin's reasons for believing in evolution. Owen may have drawn somewhat the same conclusions, but for many years Darwin thought that Owen was not an evolutionist. They had serious discussions about the principles of morphology and other important topics.

Leonard Jenyns was a good friend of Darwin when they were at Cambridge. He was also the

brother in law of Henslow. Darwin was very fond of Jenyns, and named one of his sons after him. Although not a prolific writer on natural history topics, Jenyns published some important papers on the principles of classification while Darwin was still on the *Beagle*. An invited report to the British Association for the Advancement of Science reviewed the higher systematics of animals since Cuvier's work of 1817 (Jenyns 1835). An essay written early in 1836 (Jenyns 1837) endorsed the theological approach to systematics that was common at the time. That is hardly surprising for a clergyman. Jenyns described the fishes of the voyage (Jenyns 1840–1842). Darwin's Galápagos fish collection was preserved intact, whereas some of his other collections were damaged, and therefore useless.

FIGURE 2. (G) Joseph Dalton Hooker, 1817–1911, (H) Leonard Jenyns, 1800–1893, (I) Charles Lyell, 1797–1875, (J) Alfred Russel Wallace, 1823–1913, (K) George Robert Waterhouse, 1810–1888, and (L) Hewett Cottrell Watson, 1804–1881.

In 1844, Darwin completed a draft of a book on evolution by natural selection, generally known as the *Essay* of 1844. He was afraid that he might not live to see it published. On July 5, 1844 he wrote a letter to his wife, requesting that funds be provided for having it edited and published. That raised the question of who the editor or literary executor might be. Darwin evidently had Jenyns in mind as one possibility. A few months later, on October 12, 1844, Darwin wrote a letter to Jenyns informing him that he had concluded that species are mutable "& that allied species are co-descendants of common stocks." He gave no further details, and added that he would not publish for some time. On November 25, 1844, Darwin again wrote to Jenyns, giving details of how he became an evolutionist. Those include the relationship between the Galápagos Archipelago and South America. Darwin told him about the *Essay*, and suggested that he might read it at some later time. We should note that the *Essay* itself does not say much about the Galápagos. About a year before the Darwin-Wallace papers, Jenyns suggested that varieties might become permanent (Jenyns 1857). Darwin did not conceal the fact that he was interested in species and planned to write a book about them. In May of 1848 he wrote to his neighbor, the architect and amateur botanist Edward Cresy the younger (1823–1870) "The Barnacles will put off my species book for a rather long period." As we shall see, quite a number of persons knew about Darwin's plan to publish.

We need to backtrack now and consider Darwin's relationship with two botanists: his Cambridge teacher John Stephens Henslow and his close friend Joseph Dalton Hooker. Darwin wanted Henslow to work up the *Beagle* plant collections, but although Henslow began to do so, his efforts were hampered by other commitments (Porter 1980). Hooker met Darwin briefly at the Royal College of Surgeons on January 22, 1839 (Porter 1993). Having been presented a copy of the proofs of Darwin's *Journal*, and later a copy of the published book, Hooker became a great admirer of Darwin even before he departed, on September 18, 1839, for a major scientific voyage to the southern hemisphere, as surgeon and naturalist on H.M.S. *Erebus* (Huxley 1918).

Hooker returned to England on September 7, 1843. He commenced work on the Galápagos plants toward the end of that year. An extensive correspondence between him and Darwin about biogeography soon began. On December 12, 1843, Darwin wrote to Hooker about plant distribution. He said that it is important to note from which island the Galápagos plants come from, for reasons explained in the *Journal of Researches*. Not long afterward Hooker wrote back that the Galápagos plants were exceedingly numerous. Their occurrence on separate islands Hooker considered "A most strange fact.. & one which quite overturns our preconceived notions of species radiating from a centre & migrating to any xtent [*sic*] from one focus of greater development." In other words, the facts shot down the Lyellian biogeography. Note that Darwin told Hooker what to look for and why. Hooker did as requested, and got the point.

On January 11, 1844, Darwin wrote informing Hooker of his evolutionary views, though not explaining natural selection. Early that year they corresponded extensively on biogeographical topics, including the Galápagos flora. Toward the end of that same year they discussed Lamarckian notions, and the notorious *Vestiges of the Natural History of Creation* (Anonymous [Chambers] 1844) This popular book, which presented a version of Lamarckianism combined with numerological notions, tended to give evolution a bad reputation in the eyes of professional scientists. Hooker paid the first of many visits to Down House on December 8 and 9, 1844. Although Darwin had finished his *Essay* about six months earlier that year, Hooker did not see it until 1847.

In 1845, when Darwin prepared the second edition of the *Journal of Researches*, Hooker provided Darwin with important results right up to the time that Darwin was revising the proofs. Subsequently, Hooker continued to work on the Galápagos flora. Darwin and he discussed it both in correspondence and in person. The discussion of course went far beyond just the Galápagos.

Although Hooker must have known that Darwin planned to write a book on evolution (letter from Darwin to Hooker, written on November 5 or 12, 1845), Darwin did not provide Hooker with a copy of the *Essay* of 1844 until early in 1847 (probably January 23.) Hooker's letter of March 4, 1847, commenting on the *Essay*, indicates that he was little prepared to respond to the idea of natural selection. Hooker interpreted evolution from a teleological point of view. He believed that God supervises evolution, and that rudimentary organs are present in anticipation of future use.

Hooker came to accept Darwin's theory of evolution by natural selection, but only as a result of much discussion and research experience over a period of several years. As late as April 6 & 7, 1850, Hooker in a letter to Darwin, wrote that Darwin's theories had possessed but not converted him. That did not prevent Darwin from getting what he really needed, which was advice, criticism, and experiential evidence. What mattered at that stage was having an understanding of the theory, not necessarily accepting it. Hooker did come to understand and endorse Darwin's theory. Hooker's publications, especially those on the Galápagos, were instrumental in getting it accepted.

During the period after he had completed the barnacle monograph Darwin requested information from others and did extensive experimental research of his own. One study that he undertook related to his ideas about the possible dispersal of vascular plants to oceanic islands, of which the Galápagos archipelago is obviously an example. He needed to confront the notion that the islands

had been connected by land bridges. He experimented on the effects of seawater on seeds and found that they can survive for a considerable period of time. In his first report, published on May 26, 1855, he explains that the experiments bear upon "a very interesting problem, ..., namely, whether the same organic being has been created at one point or many on the face of our globe." The following quote gives a hint of the Darwinian ecology: "But when the seed is sown in its new home then, as I believe, comes the ordeal: will the old occupants in the great struggle for life allow the new and solitary immigrant room and sustenence?" (Darwin 1855:357.) At that time Darwin was also doing experimental ecology.

On April 25, 1855, Darwin wrote a letter to the American botanist Asa Gray (1810-1888), whom he had met for a second time during a visit to Kew in 1851, asking for help with plant distribution. Darwin informed Gray of his evolutionary views in a letter dated July 20, 1857. Darwin had been investigating the role of extinction in producing geographically disjunct groups of organisms. Gray, in a letter dated July 7, 1857 wrote: "I never yet saw any good reason for concluding that the several species of a genus must ever have had a common or continuous area. Convince me of that, or show me any good grounds for it (beyond the mere fact that it is generally the case) — i.e. show me why it *ought* to be so, and I think you would carry me a good way with you — as I dare say you will, when I understand it." In order to continue the dialogue, Darwin had to explain speciation, and he did just that. Finally, on September 5, 1857, Darwin wrote Gray a letter with an appendix explaining natural selection. The appendix was included in the joint communication by Darwin and Wallace to the Linnean Society on July 1, 1858.

How about Wallace? They began to correspond because Darwin was seeking data that would support his theories. Wallace had long been an evolutionist and in 1855 published a paper entitled "On the Law which has regulated the Introduction of New Species." The upshot of this publication was that Wallace had understood the relationship between geographical distribution and speciation. He used the Galápagos biota as an example of something that his hypothesis would explain (Wallace 1855:145). Evidently the paper was largely ignored, but not by Lyell or Edward Blyth, both of whom called Darwin's attention to it (Darwin to Wallace, December 22, 1857). In a letter to Wallace dated May 1, 1857, Darwin wrote that he agreed with most of what Wallace said. Darwin related that he had been working on the topic for twenty years and that he was writing a book, but that it probably would not go to press for another two years. Telling Wallace at that time that he was writing a book on species was nothing extraordinary. It was widely known among Darwin's friends, relatives and professional colleagues. For example, he discusses progress on it in letters to his second cousin William Darwin Fox (1805–1880), written on February 8, 1857 and April 30, 1857. Lyell had become much interested in species and the possibility of evolution (Wilson 1970). On April 16, 1856, Darwin explained natural selection to Lyell when the Lyells visited the Darwins at Down House (April 13 to 16, 1856). Lyell was concerned for Darwin's priority and urged him to publish a preliminary statement. Fox recommended against that, and Darwin told Fox that he had decided to go ahead with the full treatment (Darwin to Fox, October 3, 1856). Hooker gave Darwin the same advice. On the other hand, Hewett Cottrell Watson (1804–1881) urged him to follow Lyell's advice (Watson to Darwin, June 5, 1856). Darwin's associates and correspondents who were told that he was collecting information about the origin and variation of species and with whom he shared his doubts on species variability have been listed by Porter (1993, Table 2).

Of course, had Darwin taken Lyell's advice, and come out with a preliminary statement, there would never have been the situation that arose when Wallace sent Darwin a draft of a manuscript on evolution by natural selection. The paranoid account of their relationship would have it that Darwin was beholden to Wallace for some element in his theory. But given that Wallace had read the *Journal of Researches*, and knew that Darwin was an evolutionist, we might better credit Wallace

for having understood what Darwin was talking about and then taken the next step. The fact that neither Darwin's nor Wallace's elliptical sketches evoked a serious discussion of the theory tells us once again how novel it was. The theory had to be explicated in detail and linked up to concrete examples before its explanatory prowess could be appreciated.

The Galápagos Archipelago played a major role in Darwin's explicit arguments in *The Origin of Species*, in which there is a section entitled "On the Inhabitants of Oceanic Islands" (Darwin, 1859:388–406.) The Galápagos biota now could take its place as a superb example — indeed, a living symbol — of evolution in action. But however eagerly the book had been awaited by the scientific community, the *Origin* took all of its readers by surprise — for it placed the Galápagos within the context of a new vision of the universe as a whole. On December 24, 1860, Wallace wrote a letter about the *Origin* to Henry Walter Bates (1825–1892), with whom he had sought for evidence of evolution in the Amazon Basin. We read: "Mr. Darwin has created a new science and a new philosophy, and I believe that never has such a complete illustration of a new branch of human knowledge been due to the labours and researches of a single man. Never have such vast masses of widely scattered and hitherto disconnected facts been combined into a system, and brought to bear upon the establishment of such a grand and new and simple philosophy!" (Marchant 1916:59.) Wallace realized full well that Darwin's science was an integral part of Darwin's philosophy.

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Darwin: The Botanist on the *Beagle*

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Contrary to popular belief, Charles Darwin was not hired to be the naturalist for HMS *Beagle*, nor was he deficient in training in botany, zoology, or geology. Much of this training was in botany under the tutelage of Professor John Stevens Henslow, while Darwin was a student at the University of Cambridge. His training continued during the voyage via advice sent in Henslow's letters to Darwin. As a result Darwin collected plants, algae, lichens, and fungi and made observations on vegetation almost everywhere he went on the voyage. By the time he reached the Galápagos Islands, four years into the voyage, Darwin had collected plant specimens from the Cape Verde Islands to Brazil and some of its Atlantic Islands, Uruguay, Argentina, Patagonia, Tierra del Fuego, the Falkland Islands, and Chile. After leaving the Galápagos he apparently collected plants only on the Indian Ocean's Cocos (Keeling) Islands. The importance of these collections and observations to Darwin and the floristic botanists who followed him, like Henslow and his friend William Jackson Hooker, and especially Hooker's son Joseph Dalton Hooker is emphasized, particularly those made in the Galápagos.

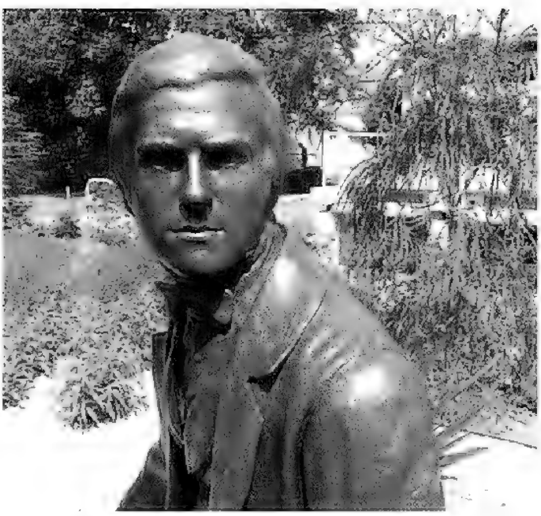

FIGURE 1. Charles Darwin at age 22 before he sailed on the *Beagle* voyage. Sculpture in the new Darwin Garden at Christ's College, Cambridge, where he was a student from January 1828 to June 1831. Sculpted by Christ's student Anthony Smith, unveiled on Darwin's 200th birthday, 12 February 2009. (Author's photo).

It is now recognized that Charles Darwin (Fig. 1) was invited by Commander Robert FitzRoy, captain of HMS *Beagle*, primarily to accompany him on a surveying voyage to southern South America (Fig. 2) as a companion and secondarily as a naturalist. The official naturalist was the Ship's Surgeon, Dr. Robert MacCormick, as was the case on British survey ships. Because of disagreements with FitzRoy and jealousy of Darwin, MacCormick left the *Beagle* in Rio de Janeiro, and Darwin *de facto* became the Ship's Naturalist. The relationships among Darwin, FitzRoy, and MacCormick are given in detail by Browne (1995:202–210).

Darwin's training in zoology commenced while he was a student at Edinburgh University. The zoological lecturer Dr. Robert Grant taught Darwin to observe, collect, and dissect marine invertebrates. He learned how to skin and dry birds from the freed slave John Edmonstone in the University's Natural History Muse-

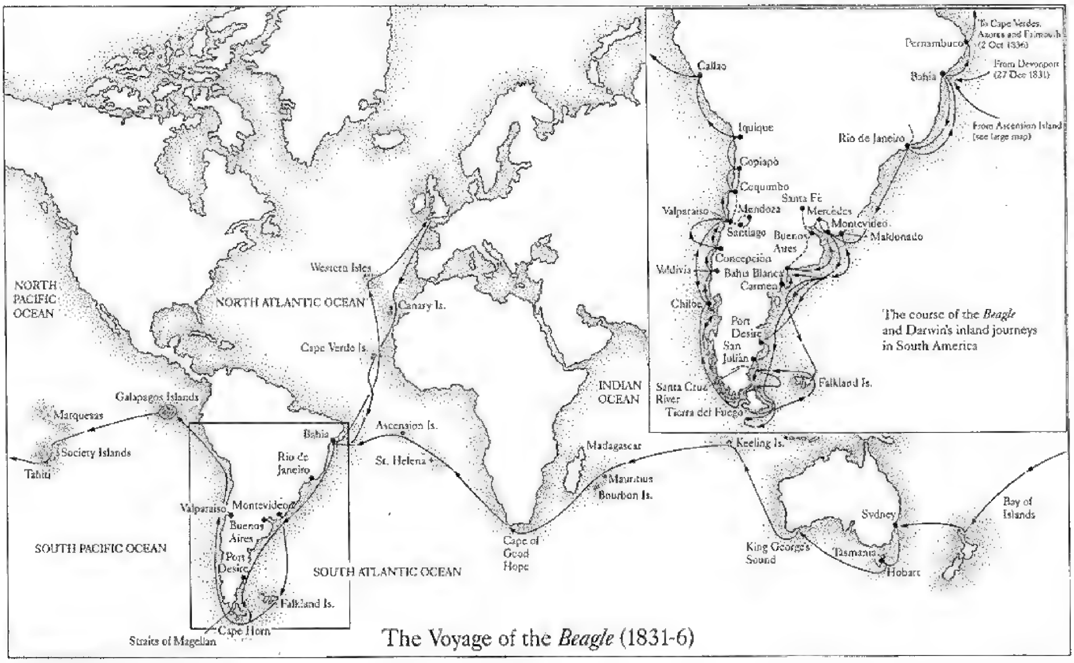

FIGURE 2. Map of the *Beagle*'s circumnavigation of the world, December 1831 to October 1836. (Image courtesy of Google Maps)

um; Darwin had long ago learned how to shoot them. At the University of Cambridge he learned to collect and appreciate insects from his second cousin and fellow student William Darwin Fox. Darwin diligently pursued all these animal interests and more on the voyage.

Although in his *Autobiography* Darwin claimed to find the geology lectures of Edinburgh's Regius Professor of Natural History Robert Jameson "incredibly dull" (Barlow 1958:52) there is evidence that his relationship with Jameson was more complicated and intimate than Darwin later admitted (Secord 1991). In addition, the influence of Henslow on Darwin's geological interests was heightened by his having been Professor of Mineralogy at Cambridge before becoming Professor of Botany. It was also Henslow who asked his good friend Adam Sedgwick, Woodwardian Professor of Geology at Cambridge, that Darwin accompany him on a three-week field trip to North Wales in August 1831, fortuitously just before Darwin was asked to participate in the *Beagle* voyage. Having recently read Darwin's notes from this field trip, I am convinced that this experience and his subsequent reading of Sir Charles Lyell's first volume of *Principles of Geology* (Lyell 1830) turned him into a real geologist. Darwin's interests in geology before, during, and after the voyage are well covered in Herbert (2005).

Ever since the original publication of Darwin's autobiography (F. Darwin 1887), it has been generally acknowledged that Henslow was the major influence on him at Cambridge. Darwin attended Henslow's botany lectures each year during the three years he was a student there, including the labs and field trips. Henslow also held a weekly open house for undergraduates and professors in science that Darwin regularly attended. Darwin famously wrote that,

> Before long I became well acquainted with Henslow, and during the latter half of my time at Cambridge took long walks with him on most days; so that I was called by some of the dons "the man who walks with Henslow"; and in the evening I was very often asked to join his family dinner. [Barlow 1958:64]

Henslow also taught Darwin to observe, dissect, and gather and press plant specimens. His first known collection in Cambridge University Herbarium was made in Wales on the trip with Sedgwick mentioned above. What was not known until recently is that Henslow implanted in Darwin an appreciation for variation within and between plant populations that eventually led him from a belief in special creation to the evolution of species (Kohn et al. 2005).

At one locality on the voyage, Bahía Blanca, Argentina, over a period of several weeks in September and October 1832, Darwin made 13 collections of a single grass species (*Poa ligularis*) (Fig. 3). Two more collections were made at nearby Monte Hermoso. Subsequently, they were identified as members of three different genera, and two different species and four different varieties of *Poa*. They show much morphological variation, and Henslow had separated them into 15 different groups, but had not applied names to them. They were identified by other botanists. Darwin wrote in his Specimen Notebook for one of these collections: "A very abundant grass, growing in tufts on sandy plains." A twentieth century flora of the region indicates that, "es común en la estepa, siendo una especia muy plástica" [it is common on the steppe, being a very variable species] (Porter 1986:39). Although vegetationally variable, close examination of their small flowers and fruits shows all to be the same species. Nevertheless, they are a good example of what Henslow was trying to instill in Darwin, an appreciation of variation.

Darwin's Specimen Labels, and Notes on the Plants

The labeling of Darwin's *Beagle* specimens is discussed in detail by Porter (1986:6–7, 1987:152–153). Suffice it to say here that before the voyage Darwin had several thousand small paper labels printed in different colors. They were numbered from 0 to 999, each thousand being a different color. Thus, a white label numbered 556 would be specimen number 556, while a red label with the same number would be 1,556. Paper labels were used for dried specimens, while specimens preserved in "spirits of wine" were affixed with small, numbered metal tags. I have only seen one of Darwin's vascular plant specimens with a paper label attached to it, at Cambridge University Herbarium. After Henslow received Darwin's plants, he went through them, removed Darwin's labels, wrote their numbers and any other label information on herbarium sheets to which he attached the plants, and gave them his own numbers (see below). In a few instances Darwin prepared field labels that survive, usually made from newsprint, that record plant name, locality, and date, and bear his signature.

When J.D. Hooker later was examining the Galápagos specimens, he wrote to Darwin (19 November 1845) that, "There are not more than two numbers to all the Gal. Collection that I can find. I have often tried to make your notes hinge on to the species. I wish you would come & take a look at them before I return them to Henslow." Darwin answered (21 November 1845): "I feel sure I sh^{d}. not be able to tell you anything about my Galapagos plants, as my numbers are gone, otherwise, of course, I w^{d} make a point of coming to Kew on purpose.—" (Burkhardt and Smith 1987:269, 271).

Darwin had sent his specimens, including plants, collected earlier in South America directly to Henslow in Cambridge via His Majesty's Navy (Porter 1985). In January 1836, after receiving the last shipment of specimens, sent from Valparaiso, Chile by Darwin in June 1835, but before Darwin returned in October 1836, Henslow arranged and drew up a list of the dried plant specimens (Porter 1986). He followed the Natural System of Classification of the Swiss botanist Alphonse de Candolle, which he used in his Cambridge Botany classes (Henslow 1828, 1829). Henslow's list was found at Cambridge University Herbarium in 1980; it is titled "Collection of plants from S. America / from C. Darwin" and is in a notebook titled "C. Darwin / Plants from S. America"

FIGURE 3. Type specimen (isolectotype) of a meadow grass (*Poa ligularis* Nees ex Steudel; Poaceae) at Cambridge University Herbarium that Darwin collected at Bahia Blanca, Argentina, in October 1832. Widespread in Argentina; also in Brazil. (Image courtesy of Cambridge University Herbarium)

(Porter 1981, 1982). It is numbered from 1 to 633, but there are 27 additional numbers designated "bis" (twice; i.e., another collection of the same species; I have found about a dozen others in herbaria thus marked, but not on this list), and 542 is given twice. The list includes flowering plants, gymnosperms, ferns, mosses, liverworts, and a few fungi. Only a few of the entries are given names by Henslow, no Galápagos collections are on the list, and no separate list of plants that Darwin collected after he left Chile has been found.

Henslow had known William Jackson Hooker, Regius Professor of Botany at Glasgow University, since 1826, and they soon began exchanging herbarium specimens (Walters and Stow 2001). Henslow wrote to Hooker on 24 November 1835 that,

> So soon as I have done with proof sheets of my little vol. in Lardner [Henslow, 1836; a volume of Dionysius Lardner's *Cabinet Cyclopaedia*] & have looked over & distributed my annual acquisitions in British Botan. I mean to have a regular attack upon Darwin's plants, & will send you specimens of all that I can. [Porter 1980a:517–518, 1984b:107]

Henslow apparently began corresponding with Hooker about Darwin's plants in August 1835. William Hooker's role in identifying some of these plant collections is discussed in detail elsewhere (Porter 1984b). Suffice it to say here that duplicate specimens were sent to Hooker in Glasgow, who, along with colleagues, described flowering plants (e.g., W.J. Hooker 1836a), mosses (e.g., W.J. Hooker 1836b), and lichens (Taylor 1847).

A second list of Darwin's collections found with Henslow's list at Cambridge University Herbarium in December 1980 was titled "Plants" in Darwin's handwriting (Porter 1981, 1982). It is in the hand of Syms Covington, Darwin's servant on the voyage, and lists all of Darwin's plant and fungal specimens to which he gave a collection number in his Specimen Notebooks. These Plant Notes are similar to those that were made for birds, fish, insects, mammals, molluscs, and reptiles and amphibians for the taxonomists who Darwin expected to identify his collections for him. All were compiled from his *Beagle* Specimen Notebooks and Zoological Notes and are written on paper watermarked "J. Whatman 1834", which according to the late Sydney Smith was purchased at the Cape of Good Hope by Darwin in June1836 (Porter 1982). Thus, they were written at sea at about the same time that Henslow was compiling his notes. The Plant Notes are discussed in detail elsewhere (Porter 1982). They are mentioned at relevant places in the following section of this paper.

It is curious that all Darwin's rock, fossil, and animal collections are labeled or tagged with a number, while only about one tenth of his plant collections are so labeled. It can be seen in the next section that he appears to start his plant collections in the Cape Verde Islands by numbering each specimen, but soon he seems only to number those that he makes an observation about in his Specimen Notebooks. Or perhaps he only numbers those of special interest. Henslow wrote to him in January 1833, in a letter with comments on plant collecting methods, that, "a single label *per month* to those of the same place is enough except you have plenty of spare time or hands to write more." (Burkhardt and Smith 1985:293). However, this letter was received by Darwin only in July 1834, long after he had done the bulk of his plant gathering. It must be assumed that Henslow was reiterating an earlier instruction to his protégé.

The Voyage

It is not surprising to find that Darwin collected so many plant specimens from unknown, out-of-the-way localities, especially islands visited by the *Beagle*. It may seem strange that he did not collect vascular plants in Peru, Tahiti, New Zealand, Australia, Mauritius, South Africa, St. Helena, Ascension Island, or the Azores, but these places, unlike the foregoing, had already been visit-

ed by numerous naturalists, and their floras were comparatively well known for the time. His perspective was shown in a letter to Henslow of 28–29 January 1836 from Sydney, "During the remainder of our voyage, we shall only visit places generally acknowledged as civilized & nearly all under the British Flag. There will be a poor field for Nat: History & without it, I have lately discovered that the pleasure of seeing new places is as nothing." (Burkhardt and Smith 1985:485).

The one exception is the Cape Verde Islands, where numerous specimens had been collected by a number of naturalists on their way to West Africa (Porter 1983). However, this being his first landfall after leaving England and there being a number of blooming plants, Darwin must have felt compelled to collect all he could find in flower. Another reason for his only collecting plants in the Galápagos and Cocos (Keeling) islands after leaving Valparaiso, Chile is that he had no way to send his specimens back to Henslow as he had done eight or nine times from South America via the British Navy earlier in the voyage (Porter 1985). In addition, he had limited space on the *Beagle* for storing them and probably had almost filled it with the rocks, animals, and plants he collected in the Galápagos.

After sending his first shipment of specimens to Henslow from 'Montevideo,' Uruguay, Darwin wrote to him in a letter of 23 July–15 August 1832 that,

> As for my Plants, 'pudet pigetque mihi' [to my shame and disgust]. All I can say is that when objects are present which I can observe & particularize about, I cannot summon resolution to collect where I know nothing.— It is positively distressing, to walk in the glorious forest, amidst such treasures, & feel they are all thrown away upon me.— [Burkhardt and Smith 1985:251]

Henslow answered in a letter of 15–20 January 1833 that, "So far from being disappointed with the Box — I think you have done wonders — as I know you do not confine yourself to collecting, but are careful to describe — Most of the plants are very desirable to *me*." (Burkhardt and Smith 1985:293). Instructions then follow on how to properly prepare a plant. This letter did not reach Darwin until July 1834, but a later one of 31 August 1833, which contained the words, "The plants delight me exceedingly" (Burkhardt and Smith 1985:369), did so earlier. This elicited a response in March 1834 that,

> I am very glad the plants gave you any pleasure; I do assure you I was so ashamed of them, I had a great mind to throw them away; but if they give you any pleasure I am indeed bound, & will pledge myself to collect whenever we are in parts not often visited by Ships & Collectors.— [Burkhardt and Smith 1985:369].

Countries and Localities Visited

The following localities are discussed in the order in which their countries were visited. The names used by Darwin are given, followed by the indigenous name if different and/or the province or territory. For each of them, latitude and longitude are given, sometimes based on the first landfall, as are their areas if known. The dates of Darwin's time spent at them follow. The known flora is given, as are the particulars of Darwin's collections, including how many of them were described as new species, subspecies, or varieties by Henslow and others. Individual species and specimens are discussed in detail by Porter (1980b, 1986, 1987, 1999) and Porter, et al. (2009). Then follow excerpts from Darwin's diary (Keynes 1988), with a pertinent observation on plants or vegetation; for the Galápagos all such comments are included. Finally, there are relevant excerpts from his letters, when they are available.

In addition to the specimens enumerated below, Darwin also collected seeds in Argentina, Chile, and Uruguay and sent them to Henslow, who planted them at Cambridge University Botan-

ic Garden and made herbarium specimens of those that germinated and grew. These specimens are in Cambridge University Herbarium and are discussed by Porter (1986, 1987, 1999) and Porter et al. (2009). Digital images of all Darwin's herbarium specimens at Cambridge are now available online in Darwin's Plants from the *Beagle* Voyage (2009) (*www.darwinsbeagleplants.org/Darwin/Home.aspx*).

Cape Verde Islands (Ilhas do Cabo Verde)

St. Jago (*São Tiago*)

14°55'N, 23°30'W; 4,033 km². Darwin visited 16 January to 18 February 1832. About 659 vascular plant species, 92 are endemics, (Frodin 2001). Darwin collected 52 species, four were new (Fig. 4), 16 bear his collecting numbers (52 collections; 66 herbarium sheets, nine of which are type specimens).

"The road to Ribera for the first six miles is totally uninteresting & till we arrived at the valley of St Martin the country presented its usual dull brown appearance: here our eyes were refreshed by the varied & beautiful forms of the tropical trees. The valley owes its fertility to a small stream & following its course Papaw trees, Bananas & Sugar cane flourished.— I here got a rich harvest of flowers, & still richer one of fresh water shells.—" (26 January, Ribera Grande). "Employed in working at yesterdays produce." (27 January). (Keynes 1988:29, 30).

In a letter of 18 May–16 June 1832 from Rio de Janeiro, Darwin wrote to Henslow that,

> One great source of perplexity to me is an utter ignorance whether I note the right facts & whether they are of sufficient importance to interest others.— In the one thing collecting, I cannot go wrong.— St Jago is singularly barren & produces few plants or insects.— so that my hammer was my usual companion, & in its company most delightful hours I spent.— [Burkhardt and Smith 1985:230]

Brazil

Fernando de Noronha Islands

3°50'N, 50°13'W; about 19 km². Darwin visited 20 February 1832. Number of vascular plant species unknown, but endemism is low (Frodin 2001). Darwin collected nine species, two new (Fig. 5) (nine collections; 14 herbarium sheets, three of which are type specimens).

"I spent a most delightful day in wandering about the woods.— The whole island is one forest, & this so thickly intertwined that it requires great exertion to crawl along.— The scenery was very beautiful, & large Magnolias & Laurels & trees covered with delicate flowers ought to have satisfied me.— But I am sure all the grandeur of the Tropics has not yet been seen by me.—" (Keynes, 1988:39). No magnolias or laurels were collected.

Darwin wrote to his father (Robert Waring Darwin) on 26 February that, "The landing there was attended with so much difficulty owing [to] a heavy surf, that the Captain determined to sail the next day after arriving." (Burkhardt and Smith 1985:203).

Bahia (*Salvador; Prov. Bahia*)

12°58'S, 38°29'W; Province of Bahia 566,979 km². Darwin visited 28 February to 18 March 1832. Number of vascular plant species in province 5,000 to 10,000 (Frodin 2001). Darwin collected 58 species (58 collections, 70 herbarium sheets).

"I walked with the two Mids[hipmen] a few miles into the interior. The country is composed of small hills & each new valley is more beautiful than the last.— I collected a great number of

FIGURE 4. Type specimen (isolectotype) of an endemic bellflower (*Campanula jacobaea* C. Smith ex Webb; Campanulaceae) at Cambridge University Herbarium that Darwin collected on Ilha São Tiago, Cape Verde Islands, in January or February 1832. (Image courtesy of Cambridge University Herbarium)

FIGURE 5. Type specimen (holotype) of an endemic pisonia (*Pisonia darwinii* Hemsley; Nyctaginaceae) at Cambridge University Herbarium that Darwin collected on Ilha Fernando de Noronha, Brazil, on 20 February 1832. (Image courtesy of Cambridge University Herbarium)

brilliantly coloured flowers, enough to make a florist go wild.— Brazilian scenery is nothing more or less than a view in the Arabian Nights, with the advantage of reality.—" (Keynes 1988:42–43).

Abrolhos Archipelago (Prov. Bahia)

Near 18°S, 39°W; 913 km², including coral reefs. Darwin visited 29 March 1832. Number of vascular plant species unknown. Darwin collected seven species (seven collections, 10 herbarium sheets).

"Two parties landed directly after breakfast. I commenced an attack on the rocks & insects & plants.— the rest began a more bloody one on the birds.—" (Keynes 1988:48). Darwin does not mention the coral reefs; he did not recognize their importance to his research program until later in the voyage.

In a letter from Montevideo to Henslow of 23 July–15 August 1832, Darwin wrote that, "My collection from the Abrolhos is interesting as I suspect it nearly contains the whole flowering Vegetation, & indeed from extreme sterility the same may also be said of St Jago—" (Burkhardt and Smith 1985:251).

Rio de Janeiro (Prov. Rio de Janeiro)

22°53'S, 43°17'W; Province of Rio de Janeiro 43,653 km². Darwin visited 5 April to 3 July 1832. Number of vascular plant species unknown. Darwin collected 13 species (13 collections, 17 herbarium sheets). Most are ferns and clubmosses of wet habitats, several others are cultivated species that could have been collected in the Rio de Janeiro botanic garden.

"Walked to the Botanic Garden [27 May], this name must be given more out of courtesy than anything else; for it really is solely a place of amusement.— The chief & great interest it possesses, is the cultivation of many plants which are notorious from their utility.— There are some 164 acres covered with the Tea tree.— I felt quite disappointed at seeing an insignificant little bush with white flowers & planted in straight rows.— Some leaves being put into boiling water, the infusion scarcely possessed the proper tea flavour.—" (Keynes 1988:67–68). *Camellia sinensis* (Theaceae) is one of the species he collected in the Botanic Garden; perhaps he did not know that the leaves needed to be fermented before becoming palatable.

ARGENTINA

Bahía Blanca (Prov. Buenos Aires)

38°45'S, 62°15'W; Province of Buenos Aires 307,571 km². Darwin visited Bahía Blanca 7 September to 17 October 1832. Number of vascular plant species unknown; Argentina has 9,620 (Frodin 2001). Darwin collected 72 species, 12 new (Fig. 3), nine bear his collecting numbers (75 collections; 173 herbarium sheets, 26 of which are type specimens).

"Took a long walk in a straight line into the interior [11 October]; uninteresting as the country is, we certainly see it in by far the best time. It is now the height of Spring; the birds are all laying their eggs & the flowers in full blossom.— In places the ground is covered with the pink flowers of a Wood Sorrell & a wild pea, & dwarf Geranium.— Even with this & a bright blue sky, the plain has a dreary monotomous aspect.—" (Keynes 1988:110). The *Oxalis* (wood sorrel; Oxalidaceae), *Lathyrus* or *Vicia* (wild pea; Fabaceae), and *Erodium* (dwarf geranium; Geraniaceae) were all collected by him here.

In his letter of about 26 October to 24 November 1832 from Montevideo, Darwin wrote to

Henslow while preparing a shipment of specimens that, "I think the dried plants nearly contain all which were then [in] Bahia Blanca flowering. All the specimens will be packed in casks.—" (Burkhardt and Smith 1985:281).

Monte Hermoso (*Prov. Buenos Aires*)

38°56'S, 61°21'W. Darwin visited on 19 October 1832. Number of vascular plant species unknown. Darwin collected 21 species, one new, this one bears his collecting number (21 collections, 36 herbarium sheets, two of which are type specimens).

"The Captain landed for half an hour at Monte Hermoso, (or *Starvation* point as we like to call it) to make observations.— I went with him & had the good luck to obtain some well preserved fossil bones of two or three sorts of Gnawing animals.—" (Keynes 1988:110). But there are no comments on plants.

Good Success Bay (*Bahía Buen Suceso; Prov. Tierra del Fuego*)

54°48'S, 65°15'W. Darwin visited 17 to 20 December 1832 and 24 to 25 February 1833. Number of vascular plant species unknown. Darwin collected three species, two of them new (three collections; six herbarium sheets, five of which are type specimens).

On 20 December 1832, Darwin writes of the difficulties in climbing Banks Hill:

> Between the stony ridges & the woods there is a band of peat bogs & over this the greater part of my track lay.— but nearly all the difficulty was avoided by following a regular path which the Guanacos frequent; by following this I reached in much shorter time the forest & began the most laborious descent through its entangled thickets.— I collected several alpine flowers, some of which were the most diminutive I ever saw; & altogether most throuighly [*sic*] enjoyed the walk.— [Keynes 1988:127]

At sea on 11 April 1833 after leaving the Falkland Islands, Darwin wrote to Henslow that,

> We were 23 days off Cape Horn, & could by no means get to the Westward.— The last & finale gale, before we gave up the attempt was unusually severe. A sea stove one of the boats & there was so much water on the decks, that every place was afloat; nearly all the paper for drying plants is spoiled & half of this cruizes collection.— [Burkhardt and Smith 1985:306]

On this cruise, the *Beagle* left Montevideo on 14 November 1832, arriving at the Falklands on 1 March 1833, having stopped at San Blas, Argentina and a number of localities in Tierra del Fuego. The day that the *Beagle* almost foundered was 13 January 1833. He later wrote to J.D. Hooker (12 December 1843) that, "I fear you will be much disappointed in my few plants: an ignorant person cannot collect; & I, moreover, lost one, the first, & best set of the Alpine plants.—" (Burkhardt and Smith 1986:420).

Falkland Islands

East Falkland Island

Near 52°S, 58°W; 12,172 km². Darwin visited 3 March to 5 April 1833, and 11 March to 6 April 1834. 256 vascular plant species, 14 are endemics (Moore 1968; Frodin 2001). Darwin collected 32 species, five of them new (32 collections; 67 herbarium sheets, 10 of which are type specimens).

"Took a long walk [3 March 1833]; this side of the Island is very dreary: the land is low &

FIGURE 6. Specimen of a shrubby sunflower (*Chiliotrichum diffusum* (Forster fil.) O. Kuntze; Asteraceae) at Cambridge University Herbarium that Darwin collected on East Falkland Island, in March 1833. "This is the largest tree, sometimes growing 2 or 3 feet high". A common dominant small shrub in Fuegia. (Image courtesy of Cambridge University Herbarium)

undulating with stony peaks & bare ridges; it is universally covered by a brown wiry grass, which grows on the peat.— In this tract, very few plants are found (Fig. 6), & excepting snipes & rabbits scarcely any animals.— The whole landscape from the uniformity of the brown color, has an air of extreme desolation.—" (Keynes 1988:145).

Darwin wrote to Henslow from the Falklands in March 1834 that, "There is no opportunity of sending a Cargo [of specimens]: I only send this [letter], with the seeds, some of which I hope may grow, & show the nature of the plants far better than my Herbarium." (Burkhardt and Smith 1985:371).

Argentina

Río Negro (Prov. Buenos Aires or Prov. Río Negro)

Near 40°45'S, 63°W. Darwin visited 4 to 10 August 1833. Number of vascular plant species unknown. Darwin collected one species (one collection; one herbarium sheet).

"This plain has a very sterile appearance it is covered with thorny bushes & a dry looking grass, & will for ever remain nearly useless to mankind. …The sandstone so abounds with salt, that all springs are inevitably very brackish.— The vegetation from the same cause assumes a peculiar appearance: there are many sorts of bushes but all have formidable thorns which would seem to tell the stranger not to enter these inhospitable plains.—" (Keynes 1988:163).

Port Desire (Puerto Deseado; Prov. Santa Cruz)

47°44'S, 65°56'W; Province of Santa Cruz 243,943 km². Darwin visited Port Desire 24 December 1833 to 4 January 1834. Number of vascular plant species unknown. Darwin collected 80 species, 18 of them new (80 collections; 145 herbarium sheets, 38 of which are type specimens).

"Took a long walk on the North side [24 December]: after ascending some rocks there is a great level plain, which extends in every direction but is divided by vallies.— I thought I had seen some desart looking country near B. Blanca, but the land in this neighbourhead so far exceeds it in sterility, that this alone deserves the name of a desert.— The plain is composed of gravel with very little vegetation & not a drop of water." (Keynes 1988:208).

In spite of this, he collected 80 species in eight days and later wrote to J.D. Hooker (11 January 1844) that, "The Botany of S. Patagonia (& I collected every plant in flower at the season when there) would be worth comparison with the N. Patagonian collection by [the French naturalist Alcide] D'Orbigny.—" (Burkhardt and Smith 1987:1).

Soon after leaving Port Desire, Darwin wrote to Henslow in March 1834 from the Falklands that, "I collected all the plants, which were in flower on the coast of Patagonia at Port Desire & St. Julian; also on the Eastern parts of Tierra del Fuego, where the climate & features of T del Fuego & Patagonia are united." (Burkhardt and Smith 1985:369).

Port San Julian (Puerto San Julián; Prov. Santa Cruz)

49°17'S, 67°45'W. Darwin visited Port San Julian 9 to 19 January 1834. Number of vascular plant species unknown. Darwin collected 19 species (19 collections; 32 herbarium sheets).

"Went out walking [14 January], & found some fine fossil shells.— The country precisely resembles that of Port Desire.— it is a little more uneven, & from the absence even of brackish water, there are fewer animals." (Keynes 1988:215). There is no mention of plants or vegetation.

***St. Sebastian Bay* (*Bahía San Sebastián; Prov. Tierra del Fuego*)**

53°15'S, 68°30'W. Darwin visited 14 to 21 February 1834. Number of vascular plant species unknown. Darwin collected two species, one of them new (two collections; four herbarium sheets, two of which are type specimens).

"The country here is part of Patagonia, open and without trees; further to the South, we have the same sort of transition of the two countries which is to be observed in the Straits of Magellan. The scenery here has in consequence a pretty, broken & park-like appearance.—" (Keynes 1988:221–222).

***Río Santa Cruz* (*Prov. Santa Cruz*)**

Puerto Santa Cruz, 50°03" S, 68°35'W. Darwin visited Río Santa Cruz 13 April to 12 May 1836. Number of vascular plant species unknown. Darwin collected 24 species, four of them new, 10 of which bear his collecting numbers (24 collections; 42 herbarium sheets, eight of which are type specimens).

"The country remains the same [22 April] & terribly uninteresting. the great similarity in productions is a very striking feature in all Patagonia, the level plains of arid shingle support the same stunted & dwarf plants; in the valleys the same thorn-bearing bushes grow, & everywhere we see the same birds & insects." (Keynes 1988:235). Despite these negative comments, he numbered 10 of the 24 species collected, indicating an intense interest in them.

CHILE

***Southern Part of Tierra del Fuego* (*Prov. Magallanes*)**

Darwin's herbarium sheets were printed with this general locality, those that follow were given specific localities. All of Fuegia covers 48,000 km². Darwin visited the southern part 24 December 1832 to 20 February 1833. Fuegia has 545 vascular plant species, 417 of which are native (Moore 1983; Frodin 2001). Darwin collected 57 species, 15 of which were new, and 10 of which bear his collecting numbers (59 collections; 107 herbarium sheets, 36 of which are type specimens).

In describing the dwellings of the Fuegians, Darwin wrote the following on 29 December 1832:

> [T]he wigwam is generally built on a hillock of shells & bones, a large mass weighing many tuns.— Wild celery, Scurvy grass, & other plants invariably grow on this heap of manure, so that by the brighter green of the vegetation the site of a wigwam is pointed out even at a great distance.— [Keynes 1988:130]

Apium australe (wild celery; Apiaceae) and *Oxalis enneaphylla* (scurvy grass; Oxalidaceae) are two of the species that Darwin collected or observed here.

In a letter of 13 or 20 November 1843, Darwin wrote to J.D. Hooker that, "I paid particular attention to the Alpine flowers of Tierra Del. & I am sure I got every plant, which was in flower in Patagonia at the seasons, when we were there.—" (Burkhardt and Smith 1986:408).

***Hardy Peninsula, Hoste Island* (*Península Hardy, Isla Hoste, Prov. Magallanes*)**

55°23'S, 68°11'W; the island covers 4,117 km². Darwin visited 13 to 16 February 1833. Number of vascular plant species unknown. Darwin collected three species, all of which bear his collecting numbers (three collections; six herbarium sheets).

"On the 13th, a party of eight under the command of Mr Chaffers [Master of the *Beagle*] crossed Hardy peninsula so as to reach & survey the West coast. The distance was not great, but from the soft swampy ground was fatiguing.—" (Keynes 1988:144). The walk was repeated on the 16th.

Elizabeth Island (*Isla Isabela, Prov. Magallanes*)

52°53'S, 70°44'W. Darwin visited 30 January 1834. Number of vascular plant species unknown. Darwin collected 12 species, five of which were new, and one of which bears his collecting number (12 collections; 21 herbarium sheets, 10 of which are type specimens).

"Got under weigh & beat up to Elizabeth island & there came to an anchor." (Keynes, 1988:218). There are no comments on plants or vegetation.

Cabo Negro (*Prov. Magallanes*)

52°57'S, 70°47'W. Darwin visited 31 January 1834. Number of vascular plant species unknown. Darwin collected 28 species, 11 of which were new (28 collections; 48 herbarium sheets, 22 of which are type specimens).

"The Ship came to an anchor in Shoal Harbor, but it was found inconvenient; she then doubled Cape Negro & again anchored in Lando Bay.— The boats were lowered & a party went on shore — no good water could be found." (Keynes 1988:218).

Port Famine (*Puerto Hambre; Prov. Magallanes*)

53°38'S, 70°56'W. Darwin visited 3 to 9 February and 1 to 7 June 1834. Number of vascular plant species unknown. Darwin collected one species (one collection; one herbarium sheet).

Darwin wrote on 7 February that, "Many of the trees are of a large size. I saw several near the Sedger river [Río Sedger], 13 feet in circumference & there is one 18.9 inches.— I saw a Winters bark 4'.6" in circumference.—" (Keynes 1988:220). Either he did not collect specimens of these trees, including *Drimys winteri* (winters bark; Winteraceae), or they did not survive the voyage.

Mount Tarn (*Monte Tarn, Prov. Magallanes*)

53°36'S, 71°30'W. Darwin visited on 6 February 1834. Number of vascular plant species unknown. Darwin collected five species, two of them new (five collections; eight herbarium sheets, four of them type specimens). All were collected at "2000 ft."

"I left the ship at four oclock in the morning to ascend Mount Tarn; this is the highest land in this neighbourhead being 2600 feet above the sea. For the first two hours I never expected to reach the summit.— …Our return was much easier as the weight of the body will force a passage through the underwood; & all the slips & falls are in the right direction.—" (Keynes 1988:219, 220).

Gregory Bay (*Bahía Gregorio, Prov. Magallanes*)

52°39'S, 70°14'W. Darwin visited 13 February and 29 May 1834. Number of vascular plant species unknown. Darwin collected one species (one collection; three herbarium sheets).

On 29 May, Darwin wrote in his diary that,

> We anchored in Gregory Bay & took in six days water … The Thermometer has been all day below the freezing point & much snow has fallen: This is rather miserable work in a ship, where you have no roaring fire; & where the upper deck, covered with thawing snow is as it were, the hall in your house.— [Keynes 1988:240]

Wollaston Island (Isla Wollaston, Prov. Magallanes)

55°42'S, 67°17'W. Darwin visited 25 to 26 February 1834. Number of vascular plant species unknown. Darwin collected five species, one of them new, and a different one bears his collecting number (five collections; 10 herbarium sheets, of which one is a type specimen).

"I walked or rather crawled to the tops of some of the hills; the rock is not slate, & in consequence there are but few trees; the hills are very much broken & of fantastic shapes.—" (Keynes 1988:222).

Chiloe Island (Isla de Chiloé; Prov. Chiloé)

41°51'S, 73°50'W; 8,394 km². Darwin visited 29 June to 12 July and 21 November to 11 December 1834, and 18 January to 4 February 1835. Number of vascular plant species unknown. Darwin collected 11 species, two of them new (11 collections; 18 herbarium sheets, four of which are type specimens).

On 8 December Darwin wrote: "In the lower parts of the hills, noble trees of Winters bark [*Drimys winteri*], & the Laurus sassafras (?) [Lauraceae?] with fragrant leaves, & others the names of which I do not know, were matted together by Bamboos or Canes [probably a species of the grass genus *Chusquea*].—" (Keynes 1988:273). None of these species were collected, or survived collection, probably because of the copious rainfall that Darwin also wrote about while on the island.

Darwin wrote to Henslow in a letter written between 24 July and 7 November 1834 and posted from Valparaíso that, "I suppose that the Botany both there [Chiloé] & in Chili is well known. —" (Burkhardt and Smith 1985:400).

Valparaíso (Prov. Valparaíso)

33°05'S, 71°38'W. Darwin visited 23 July to 13 August and 27 September to 9 November 1834, and 12 to 14 March and 17 to 26 April 1835. Number of vascular plant species unknown. Darwin collected 45 species (48 collections; 64 herbarium sheets).

On 5 August Darwin wrote in his diary that,

> I have taken several long walks in the country. The vegetation here has a peculiar aspect; this is owing to the number & variety of bushes which seem to supply the place of plants [perennial herbs]; many of them bear very pretty flowers & very commonly the whole shrub has a strong resinous or aromatic smell. In climbing amongst the hills ones hands & even clothes become strongly scented. [Keynes 1988:250]

However, many of the plants he collected are garden ornamentals or weeds.

After leaving Valparaíso on 14 March 1835, Darwin traveled to Santiago, Chile and over the Andes to Mendoza, Argentina. He apparently collected no herbarium specimens on this trip, but he wrote to Henslow on 18 April after his return that,

> All the flowers in the Cordilleras appear to be Autumnal flowerers,— they were all in blow & seed—many of them very pretty.— I gathered them as I rode along on the hills sides: if they will but choose to come up I have no doubt many would be great rarities.— [Burkhardt and Smith 1985:443]

Only his seeds of *Lycium chilense* var. *odonellii* (desert thorn, Solanaceae), perhaps from Mendoza (Porter 1986), germinated in the Cambridge University Botanic Garden.

Chonos Archipelago (*Archipiélago de los Chonos; Prov. Aisén*)

44°40'S, 74°18'W. Darwin visited 13 to 17 December 1834 and 8 to 14 January 1835. Number of vascular plant species unknown. Darwin collected 42 species, 14 of them new, one bears his collecting number (44 collections; 77 herbarium sheets, 29 of which are type specimens).

For 15 to 17 December, Darwin wrote:

> The weather continued bad; to me it did not much signify, because the land in all these islands is next thing to impassable … as for the woods, I have said enough about them; I shall never forget or forgive them; my face, hands, shin-bones all bear witness what maltreatment I have received in simply trying to penetrate into their forbidden recesses.—[Keynes 1988:274]

In spite of this, Darwin was able to collect a number of specimens.

Cape Tres Montes (*Cabo Tres Montes; Prov Aisén*)

46°45'S, 74°55'W. Darwin visited 22 to 27 December 1834. Number of vascular plant species unknown. Darwin collected 30 species (eight labeled "Patch Cove"), 11 of them new (30 collections; 54 herbarium sheets, 23 of which are type specimens).

"On the Monday [22 December] I succeeded in reaching the summit (1600 ft. high); it was a laborious undertaking; the ascent being so steep as to make it necessary to use the trees like a ladder." This, a marginal note ("Great thickets of Fushza [*Fuchsia magellanica* (Onagraceae)]."), and the discovery of "a bed made of grass", subsequently found to be that of shipwrecked seamen, are the only references to plants at Cape Tres Montes (Keynes 1988:274, 275).

ECUADOR

Galápagos Islands (*Archipiélago de Colón*)

7,844 km^2. Darwin visited 16 September to 17 October 1835. About 1,400 vascular plant species; 43% of the 555 natives are endemics (Tye and Francisco-Ortega, in press); 894 species are introduced (Tye, pers. comm., August 2009). Darwin collected 186 species, 97 of them new, only 14 of which bear his collecting numbers (237 collections; 350 herbarium sheets, 191 of which are type specimens). Included in these figures are 17 collections in the Herbarium of the Royal Botanic Gardens, Kew collected by Darwin, which are labeled simply "Galapagos Islands." They presumably are duplicates of specimens in the Cambridge University Herbarium, but they lack Darwin's and Henslow's numbers, and it is impossible to assign them to islands. They include 19 herbarium sheets and 15 probable type specimens. Most introduced species have arrived since Darwin's visit.

Darwin wrote to his sister Caroline from New Zealand on 27 December 1835: "My last letter was written from the Galapagos, since which time I have had no opportunity of sending another." (Burkhardt and Smith 1985:471). Unfortunately, this letter has not been found. We can scarcely imagine what he conveyed of his observations on the biology and geology of the islands in this letter, and can only hope that it will sometime be discovered, perhaps to give us further insights into Darwin's impressions of what he witnessed there.

On 28–29 January 1836, Darwin wrote to Henslow from Sydney, Australia that,

> I last wrote to you from Lima, since which time I have done disgracefully little in Nat: History, or rather I should say since the Galapagos Islands, where I worked hard.—Amongst other things, I collected every plant, which I could see in flower, & as it was the

> flowering season I hope my collection may be of some interest to you.— I shall be very curious to know whether the Flora belongs to America, or is peculiar. [Burkhardt and Smith 1985:485]

Chatham Island (Isla San Cristóbal)

00°53'S, 86°36'W; 552 km^2. Darwin visited 16 to 22 September 1835. Darwin collected 41 species, 23 of them new, seven bear his collecting numbers (42 collections; 70 herbarium sheets, 44 of which are type specimens).

FIGURE 7. Frigatebird Hill (on the right), Isla San Cristóbal (Chatham Island), Galápagos Islands, where Darwin made his first landfall in the archipelago, on 16 September 1835. The leafless vegetation looks very much like that Darwin described in his journal. (Author's photo).

FIGURE 8. An endemic gray matplant (*Tiquilia darwinii* (Hooker fil.) A. Richardson; Boraginaceae), the lectotype specimen of which was collected by Darwin at Frigatebird Hill, on 16 September 1835. (Author's photo).

"These islands at a distance have a sloping uniform outline, excepting where broken by sundry paps & hillocks.— The whole is black Lava, *completely* covered by small leafless brushwood & low trees.—...the stunted trees show little signs of life.—...The plants also smell unpleasantly." (16 September, Frigatebird Hill [Cerro Tijeretas]; Fig. 7). "When on shore I proceeded to botanize & obtained 10 different flowers; but such insignificant, ugly little flowers, as would better become an Arctic, than a Tropical country.—" (17 September, Stephens Bay; Fig. 8). "The vallies in the neighbourhead [*sic*] were coloured a somewhat brighter green.— Upon first arriving I described the land as covered with leafless brushwood; & such certainly is the *appearance*. I believe however almost every plant or tree is now in flower & its leaf.— But the most prevalent kinds are ornamented with but very few & these of a brown color." (19 and 20 September, Stephens Bay; Fig. 9). "The age of the various [lava] streams is distinctly marked by the presence & absence of Vegetation; in the latter & more modern nothing can be imagined more rough and horrid.— ...In my walk I met two very large Tortoises (circumference of shell about 7 ft). One was eating a Cactus & then quietly walked away.— ...Surrounded by the black Lava, the leafless shrubs & large Cacti, they appeared most old-fashioned antediluvian animals; or rather inhabitants of some other planet.—" (21 September, Craterized District). "We slept on the sand-beach, & in the morning after

FIGURE 9. Specimens of lecocarpus (left specimen: *Lecocarpus leptolobus* (Blake) Cronquist & Stuessy; right specimens: *L. lecocarpoides* (Robinson & Greenman) Cronquist & Stuessy; Asteraceae) at Cambridge University Herbarium that Darwin collected on Isla San Cristóbal in September 1835. The genus is endemic to the Galápagos. (Author's photo).

having collected many new plants, birds, shells & insects, we returned in the evening on board — (22 September, Finger Hill [Cerro Brujo]; Fig. 10). (Keynes 1988:351–352, 353, 354).

FIGURE 10. The endemic Galápagos tomato (*Solanum cheesmaniae* (L. Riley) Fosberg; Solanaceae), which Darwin collected on Isla San Cristóbal in September 1835. This photo of the late Dr. Robert Bowman collecting its fruits was taken on Isla Bartolomé on 3 February 1967. (Author's photo.)

Charles Island (*Isla Floreana*)

01°14'S, 96°26'W; 171 km². Darwin visited 24–27 September 1835. Darwin collected 77 species, 39 were new, two bear his collecting numbers (83 collections; 121 herbarium sheets, 65 of which are type specimens).

"The first part of the road [to the settlement at about 1,000 ft. elevation] passed through a thicket of nearly leafless underwood as in Chatham Is[d].— …The wood gradually becomes greener during the ascent.— [Fig. 11] Passing round the side of the highest hill; the body is cooled by the fine Southerly trade wind & the eye refreshed by a plain green as England in the Spring time.— Out of the wood extensive patches have been cleared, in which sweet Potatoes (convolvulus Batata) & Plantains grow with luxuriance.— Since leaving Brazil we have not seen so Tropical a Landscape, but there is a great deficiency in the absence of the lofty, various & all-beautiful trees of that country.— It will not easily be imagined, how pleasant the change was from Peru & Northern Chili, in walking in the pathways to find *black mud* & on the trees to see mosses, ferns & Lichens & Parasitical plants adhaering.— Owing to an unusual quantity of rain at this time of year, I suspect we have seen the Island at its full advantage.—" (25 September, Post Office Bay). "I industriously collected all the animals, plants, insects & reptiles from this island.— It will be very interesting to find from future comparison to what district or 'centre of creation' the organized beings of this archipelago must be attached.— I ascended the highest hill on the Is[d], 2000 ft. [Round Hill (Cerro Pajas), 640 m]— it was covered in its upper part with coarse grass & Shrubs.— [Fig. 12] …It is long since the Lava streams which form the lower parts of the Island flowed from any of these Craters: Hence we have a smoother surface, a more abundant soil, & more fertile vegetation.—" (26 and 27 September, Black Beach). (Keynes 1988:355, 356).

FIGURE 11. An endemic fleabane (*Erigeron tenuifolium* Hooker fil.; Asteraceae), the lectotype specimen of which Darwin collected on Isla Floreana (Charles Island) in September 1835. Until recently, it was placed in an endemic genus, *Darwiniothamnus*. (Author's photo.)

Neither the sweet potato (*Ipomoea batatas*; Convolvulaceae) nor the plantain (*Musa paradisiaca*; Musaceae) were collected. However, Charles Island did yield the type specimen of an endemic "Parasitical" plant, *Phoradendron henslovii* (Viscaceae), named by Hooker for Henslow (Fig. 13).

FIGURE 12. An endemic wild coffee (*Psychotria angustata* Andersson; Rubiaceae), syntype specimens of which Darwin collected on Floreana, in September 1835. It had not been recollected since the Swedish botanist N. J. Andersson's visit in July 1852, until it was rediscovered in an area on Floreana protected from goats in 1982. (Author's photo.)

FIGURE 13. The endemic mistletoe (*Phoradendron henslovii* (Hooker fil.) Robinson; Viscaceae), the holotype specimen of which Darwin collected on Floreana, in September 1835. "Parasite — growing on various kinds of trees". (Author's photo.)

Albemarle Island (*Isla Isabela*)

00°52'S, 91°30'W; 4,670 km². Darwin visited 1 October 1835. Darwin collected 10 species, four of them new (Fig. 14) (10 collections; 11 herbarium sheets, five are type specimens).

"The little of the country I have yet seen in this vicinity is more arid & sterile than in the other Islands.—" (1 October, Tagus Cove; Fig. 15). "We then stood round the North end of Albermale Island.— The whole of this has the same sterile dry appearance . . . . I should think it would be difficult to find in the intertropical latitudes a piece of land 75 miles long, so entirely useless to man or the larger animals.—" (3 October, at sea). (Keynes 1988:359, 360).

FIGURE 14. The endemic romerillo (*Macraea laricifolia* Hooker fil.; Asteraceae), a paralectotype specimen of which Darwin collected on Isla Isabela on 1 October 1835. The genus is know only from this single species. (Author's photo.)

James Island (*Isla Santiago*)

00°10'S, 90°49'W; 572 km^2. Darwin visited 8–17 October 1835. Darwin collected 83 species, 42 of them new, five bear his collecting numbers (85 collections; 129 herbarium sheets, 77 of which are type specimens).

"Taking with us a guide we proceeded into the interior & higher parts of the island.... At about six miles distance & an elevation of perhaps 2000 ft the country begins to show a green color.— [Fig. 16]...Lower down, the land is like that of Chatham Is^{d}, — very dry & the trees nearly leafless. I noticed however that those of the same species attained a much greater size here than in any other part.— The Vegetation here deserved the title of a Wood: the trees were however far from tall & their branches low & crooked." A note in the page margin states that, "Saw some having circumference of 8 ft & several of 6 ft". "During the greater part of each day clouds hang over the highest land: the vapor condensed by the trees drips down like rain. Hence we have a brightly green & damp vegetation & muddy soil.— [Fig. 17] The contrast to the sight & sensation of the body is very doubtful after the glaring country beneath.— The case is exactly similar to that described in Charles Is^{d}.— So great a change with so small a one of elevation cannot fail to be striking.—" (9 October, Buccaneer Cove). "On the 12th I paid a second visit to the houses [at 2,000 ft.] ...I thus enjoyed two days collecting in the fertile region.— Here there were many plants, especially Ferns; the tree Fern however is not present. The tropical character of the Vegetation is stamped by the commonest *tree* being covered with compound flowers of the Syngynesia [Asteraceae; *Scalesia pedunculata*; Fig. 18].— ..."[The land iguanas] live entirely on vegetable productions; berrys [*sic*], leaves, for which latter they fre-

FIGURE 15. Tagus Cove, Isla Isabela (Albemarle Island), with Darwin Lake in the foreground. The leafless vegetation looks very much like that Darwin described in his journal, when he visited on 1 October 1835. (Author's photo.)

FIGURE 16. James Bay, Isla Santiago (James Island). Darwin spent nine days on Santiago, three of them in the highlands in the background. (Author's photo.)

FIGURE 17. An endemic orchid (*Epidendrum spicatum* Hooker fil.; Orchidaceae), the holotype specimen of which Darwin collected on Isla Santiago in October 1835. (Author's photo.)

quently crawl up the trees, especially a Mimosa [*Acacia* (Mimosaceae)]; never drinking water, they like much the succulent Cactus [*Opuntia* (Cactaceae)], & for a piece of it they will, like dogs, struggle [to] seize it from another. …In all these Isl[ds] the dry parts reminded me of Fernando Noronha; perhaps the affinity is only in the similar circumstance of an arid Volcanic soil, a flowering leafless Vegetation in an intertropical region, but without the beauty which generally accompanies such a position.—" (10 October, Buccaneer Cove). "The Lake is quite circular & fringed with bright green succulent plants; the sides of the Crater [Salt Mine Crater (Mina de Sal)] are steep & wooded; so that the whole has rather a pretty appearance.— …In rocky parts there were great numbers of a peculiar Cactus [*Opuntia galapageia*] whose oval leaves connected together formed branches rising from a cylindrical trunk.— In places also a Mimosa [*Acacia insulae-iacobi*] was common; the shade from its foliage was very refreshing, after being exposed in the open wood to the burning Sun.—" (11 October, Puerto Egas). "We all were busily employed during these days in collecting all sorts of Specimens." (12 to 16 October). (Keynes 1988:361, 362, 363). The plants collected included the *Opuntia* and the *Acacia*.

FIGURE 18. An endemic lechoso tree (*Scalesia pedunculata* Hooker fil.; Asteraceae), the lectotype specimen of which Darwin collected on Isla Santiago in October 1835; "the characteristic & *abundant* tree in the high ground: grows to a good size" The genus is endemic to the Galápagos. (Author's photo.)

AUSTRALIA

Keeling Islands (*Cocos* (*Keeling*) *Islands; Overseas Territory*)

12°11'S, 96°54' E; 14 km². Darwin visited 2 to 11 April 1836. There are 121 vascular plant species, 64 are native, none are endemic (Telford 1993; Frodin 2001). Darwin collected 22 species, two of them new (22 collections; 26 herbariun sheets, two are type specimens).

"Besides the Cocoa nut [*Cocos nucifera*; Arecaceae; Fig. 19] which is so numerous as at first

to appear the only tree, there are five or six other kinds. One called the Cabbage Tree [*Pisonia grandis*; Nyctaginaceae], grows to a great bulk in proportion to its height, & has an irregular figure; its wood being very soft. Besides these trees the number of native plants is exceedingly limited; I suppose it does not exceed a dozen [Fig. 20]. Yet the woods, from the dead branches of the trees, & the arms of the Cocoa nuts is a thick jungle.—" (Keynes 1988:414–415). Darwin did not collect the coconut or the cabbage tree.

On 29 April 1836, Darwin wrote to his sister Caroline from Mauritius about visiting the Cocos (Keeling) Islands. He does not mention plants or vegetation, but marvels at the first coral reef he was able to examine in detail. "The subject of Coral formation has for the last half year, been a point of particular interest to me. I hope to be able to put some of the facts in a more simple & connected point of view, than that in which they have hitherto been considered." (Burkhardt and Smith 1985:495). This subject turned into the first of his three books on geology that resulted from the voyage, *Coral Reefs* (Darwin 1842).

The next section of the paper traces the path of Darwin's Galápagos collections following his return to England.

FIGURE 19. A coconut (*Cocos nucifera* Linnaeus; Arecaceae), which Darwin described as being abundant in the Cocos (Keeling) Islands in April 1836, but which he did not collect. (Author's photo.)

After the Voyage: Henslow

On 30 October 1836, just two days after the *Beagle* arrived in Greenwich on the 28th to pay off the crew and be decommissioned, Darwin wrote to Henslow from London that,

> I have delayed writing, as I daily expected the *Beagle* would arrive, and I should be better able to tell you how my prospects go on.— I spent yesterday on board at Greenwich, & brought back with me the Galapagos plants; they do not appear numerous, but are I hope in tolerable preservation.— Tomorrow I will procure a box & will send them to Cambridge.— [Burkhardt and Smith 1985:512]

On 1 November Darwin wrote:

> You will have probably received, before this letter reaches you, the box with the Galapagos plants, which also contains a longer letter [that above]. The box starts tomorrow by the Fly Coach.— Four boxes were also sent by Marsh's Wagon today.— they will reach Cambridge on Thursday morning.— [Burkhardt and Smith 1985:515]

Before embarking on the voyage, Darwin had visited Robert Brown, keeper of the botanical collections at the British Museum, several times for advice on microscopes and perhaps on plant

FIGURE 20. Specimen of an East Indian bristlegrass (*Setaria barbata* (Lamarck) Kunth; Poaceae) at Cambridge University Herbarium that Darwin collected at the Cocos (Keeling) Islands in April 1836, which apparently has not been collected there since then. (Image courtesy of Cambridge University Herbarium.)

collecting (Barlow 1958; Burkhardt and Smith 1985). On his return to London he visited the formidable Brown again, and wrote to Henslow on 28 March 1837 that, " he asked me in rather an ominous manner, what I meant to do with my plants." (Burkhardt and Smith 1986:14). Brown had been given the plants collected by Captain Philip Parker King, commander of the first, 1826–1830, *Beagle* voyage, but he had not identified them. So Darwin was wary of giving his plants to Brown, as he was keen to use information on them in his own narrative of the voyage (Darwin 1839a), which he was now writing. Darwin was wise to be wary; later he passed on his fossil plants and some fungi to Brown, and they disappeared into the British Museum, never to be heard of again. In his letter to Henslow, Darwin also stated that, "Mr Brown also said that *you* must recollect that there are plants from the Galapagos Islds. at the Brit. Museum.— It would be well to find out what they are.—" (Burkhardt and Smith 1985:14). This apparently refers to specimens collected in 1795 by Archibald Menzies, surgeon and naturalist on HMS *Discovery*, captained by George Vancouver (Porter 1980b).

In this letter to Henslow, Darwin began a series of questions about his plants that continued until after his *Narrative* (Darwin, 1839a) was published. These include:

> At some future time I shall want to know number of species of plants at Galapagos and Keeling, and at the latter whether seeds could probably endure floating on salt water. I suppose, after a little more examination you would be able to say, what was the general character of the vegetation of the Galapagos.—? [Burkhardt and Smith 1986:14]

This interest in seeds and salt water was pursued experimentally in the 1850s and culminated in Darwin (1857). The vegetation of the Galápagos Islands is discussed in his *Narrative* (Darwin 1839a). Henslow was able to determine how many plant species were known from the Cocos (Keeling) Islands (Henslow 1838), but, as we shall see, not from the Galápagos.

On 18 May 1837, Darwin wrote to Henslow:

> There are about half a dozen plants, of which I do not know the names of genus or something about them, I must strike out long passages in my journal.— Will you have the kindness to tell me; a week or ten days before you leave Cambridge [at the end of Easter Term]; so that those questions which are most indispensible to me; perhaps you would not grudge one day in answering.— This is in case I publish before autumn, otherwise when you return will be soon enough for me.— [Burkhardt and Smith 1986:18]

Darwin presumably refers to Henslow's return to Cambridge at the beginning of Michaelmas Term in October. According to Freeman (1977), Darwin completed the manuscript of the main text of his volume of the *Narrative* by June 1837 (but see below), and it and the index were printed early in 1838; the preface and appendix were written later and probably printed before 24 January 1839. Because of delay by FitzRoy in completing the other volumes, the book itself was not published until around the beginning of June 1839 (May according to Burkhardt and Smith 1986:198).

This letter to Henslow also contained Darwin's invitation for him to write up the Galápagos plants as a part of the *Zoology of the Beagle* (Darwin 1838–1843):

> I forgot to ask you: if I succeed with government and if afterwards it appears advisable, should you object to publish the botany of the Galapagos in it: as part of the fauna?— I certainly should like, if possible, some part of the botany kept together, where there are materials for any general result.— [Burkhardt and Smith 1986:18]

Darwin obtained a grant of £1,000 from the Chancellor of the Exchequer to publish his *Zoology of the Beagle* in August 1837 (Burkhardt and Smith 1986:38–39), but the Galápagos plants were not included in that work.

On 28 May 1837, Darwin wrote to Henslow that, "The questions about plants are very few in number which I want answered, and I will copy them out on the other side.— .... I will copy out the list of Botanical questions on a separate piece of paper.—" (Burkhardt and Smith 1986:21, 22). It is not known for sure if any of these questions were about Galápagos plants, because the separate piece of paper has not been found, but the quote below from his next letter can be interpreted to indicate that there may have been some.

In contradiction to Freeman's (1977) statement that Darwin had finished his manuscript of the main text of his *Narrative* by June, Darwin wrote to Henslow on 12 or 13 July 1837 that:

> I am now hard at work, cramming up learning to ornament my journal with, you may guess the object of this letter is to beg, a few hard names, respecting my plants.— I believe I shall really begin printing in beginning of August, so that there is no time to lose.— Will you look over the list of questions, & try to answer me some of them.— ....You can tell me something about the Galapagos plants, without any further examination:— [Burkhardt and Smith 1986:31]

Darwin asked his final questions regarding his plants in a letter to Henslow of 1 August 1837, stating that, "I send my MSS to the press the day after tomorrow...." (Burkhardt and Smith, 1986:33). However, he was still writing the text, as the letter of 19 November 1837 to Henslow reveals: "My journal, I am very glad to be able to tell you is very near its end.— One more chapter, & that not a very long one, will complete the task...." (Burkhardt and Smith 1986:59).

On 16 August, Darwin wrote to Henslow that, "I really hope in the course of a week to have some proof sheets, but there has been an unavoidable delay on the part of the printers. ....The next time you hear from me, probably it will be with a proof sheet.—" (Burkhardt and Smith 1986:37). Indeed, in September and October Darwin's several letters discuss Henslow's reading of the proof sheets for Darwin (1839a), but there is no evidence of Henslow answering Darwin's questions about his plants.

As a result of Henslow's failure to supply Darwin with much information about his plant collections, the *Narrative* is " singularly sparse in botanical information" (Porter 1980a:518). However, Henslow should not be judged too harshly, as these years were a very busy period for him (Porter, 1980a). He was Professor of Botany at Cambridge and also Director of the University Botanic Garden; planning for a new garden took more time than his professorial duties. He was curating a large herbarium, planning museums in Ipswich and Cambridge, and conducting his own research on fossil plants and the British flora. In addition, in 1837 Rev. Henslow was appointed Rector of Hitcham in Suffolk, duties for which soon began to take up much of his time. "Henslow performed admirable service in getting Darwin onto the *Beagle* and in receiving his collections as they dribbled back from across the world, but he failed in his good-hearted attempts to work up the plants." (Porter 1980a:519).

Luckily for Darwin, his volume of the *Narrative* apparently sold better than the other two and was reprinted in August 1839 under the more descriptive title of *Journal of Researches* (Darwin 1839b). It was this version that the eminent Prussian naturalist and traveller Alexander von Humboldt commented on at length in a letter to Darwin of 18 September 1839. In his letter, von Humboldt stated (in translation from the French):

> Of how many things we are still ignorant[.] Observations are so incomplete. How much I regret that Mr Henslow could not finish examining your interesting collection (pp. 460 [Galapagos Islands plants], 537 [Henslow is not mentioned in this discussion of King George's Sound, Western Australia plants], 541 [Cocos (Keeling) Islands plants] if only to determine the families or the proximity of some known genera. The vegetation exhibits

> the fundamental character of a country. By tracing even the main features, one gives an image which will remain in one's mind, something like a stereotype; animals offer mobile characters. [Burkhardt and Smith 1986:428]

In a letter to Henslow of 10 November 1839, Darwin wrote:

> I am delighted to hear you have taken some of my plants with you to Hitcham.
> — I believe you have received a message I sent you saying that Humboldt in a letter to Me expresses at great length his **vivid** *regret* that M. Henslow has not been able to describe the species, or even characterize the genera of the very curious collection of plants from Galapagos— Do think once again of making one paper of the Flora of these islands … I do not think there will often occur opportunities of drawing up a monograph of more interest.— if your descriptions are frittered in different journals, the general character of the Flora never will be known, & foreigners, at least, will not be able to refer to this & that journal for the different species.— But you are the best judge.— [Burkhardt and Smith 1986:238]

Darwin's comment on frittering away descriptions in different journals refers to Henslow's treatments of Darwin's Galápagos prickly pears (Henslow 1837) and Cocos (Keeling) plants (Henslow, 1838), neither of which Humboldt apparently was aware.

At this time, according to his yearly journal (Burkhardt and Smith 1986:434–435), Darwin became immersed in editing various numbers of *Zoology of the Beagle*, reading, note-taking, and writing on his species theory, writing papers on geology and botany, writing *Coral Reefs* (Darwin 1842), and he began writing *Volcanic Islands* (Darwin 1844). Darwin also made one last attempt to wrest information about his plants from the otherwise busy Henslow. He wrote to Henslow in a letter of 22 January 1843:

> I hope indeed, you will find leisure from your weightier occupations to go on with your fossil work, & I must put in a word for poor Galapagos plants— remember the regret Humboldt expressed that you had not published some sketch of them; whenever you do so I shall be very curious to know, what sort of relation the Flora bears to that of S. America. [Burkhardt and Smith 1986:348]

Alas, this was not to be; but help was on the horizon.

After the *Beagle*: J.D. Hooker

Darwin had met Sir William Jackson Hooker, his son the botanist Joseph Dalton Hooker, and the Harvard University botanist Asa Gray together in London at the Royal College of Surgeons on 22 January 1839 (Porter 1993). Darwin and J.D. Hooker met a second time later in 1839 (Porter 1980a), when Hooker was walking in Trafalgar Square with Robert MacCormick, who for a short time had been surgeon on the *Beagle*. This was prior to Hooker and MacCormick in September sailing as assistant surgeon and surgeon, respectively, on the Antarctic voyage of H.M.S. *Erebus* and H.M.S. *Terror*, from which Hooker was not to return until September 1843. No correspondence between Darwin and Hooker during the time of Hooker's voyage has been found, but Darwin read letters of Hooker to others, which were circulated as those of his from the *Beagle* voyage had been. Hooker began to read proof sheets of Darwin's *Narrative* before and during his voyage that Darwin had sent to their mutual friend the geologist Sir Charles Lyell. Hooker wrote to his mother on 6 December 1842 that, "Indeed all Darwin's remarks are so true and so graphic wherever we go that Mr. Lyell's [Sir Charles' father] kind present is not only indispensable but a delightful companion and guide." (Porter 1993:10).

On 12 March 1843, Darwin wrote to W. J. Hooker:

> When you next write to your son, will you please remember me kindly to him & give him my best thanks for his note.— I had the pleasure yesterday of reading a letter from him to Mr Lyell of Kinnordy [Sir Charles' father] full of the most interesting details & descriptions, & written (if I may be permitted to make such a criticism) in a particularly agreeable style. ....I am very glad to hear you talk of inducing your son to publish an Antarctic Flora— I have long felt much curiosity for some discussion on the general character of the Flora of Tierra del Fuego, that part of the globe, furthest removed in latitude from us. ...I am sure I may speak on part of Prof. Henslow that all my collection (which gives fair representation of alpine flora of T. del. Fuego & of Southern Patagonia) will be joyfully laid at his disposal.— [Burkhardt and Smith 1986:351]

J.D. Hooker's note to Darwin has not been found. Perhaps it was sent to him by W.J. Hooker with his letter to which the above letter is in answer, but which also has not been found. In time, Darwin's *Beagle* plants were delivered to J.D. Hooker, and many from southern South America were described in his *Antarctic Flora* (J.D. Hooker 1844–1847). In July 1846 Darwin was to write to Hooker that,

> I have just finished your late numbers of the A. Flora & have been in truth delighted with them: ...By the way, you cannot think how proud I am at seeing how many species I collected: it has often been a vexation to me, how much trouble I threw away on some collections, amongst which I formerly ranked my plants, but now they are a real source of pleasure to me. [Burkhardt and Smith 1987:328]

Darwin had a special interest in his Galápagos specimens, which also were delivered to Hooker. I have not seen any letters between Henslow and W.J. Hooker about them, and the known letters between Henslow and Darwin of this time do not discuss them. However, several letters from Henslow to J.D. Hooker do so, the first being: "I have Darwin's *memoranda* [the Plant Notes] to bring up with me [presumably to London] — & if I can I will bring also the Galapagos plants." (9 September 1843; Porter 1980a:525). In a long letter to Hooker of 13 or 20 November 1843 about his collections, Darwin wrote:

> I hope Henslow will send you my Galapagos plants (about which Humboldt even expressed to me considerable curiosity) — I took much pains in collecting all I could,— A Flora of this archipelago would, I suspect, offer a nearly parallel case to that of St Helena, which has so long excited interest. [Burkhardt and Smith 1986:408]

In his Transmutation Notebook C, written between March and June 1838, in a note on the Canary Islands, Darwin wrote: "**Did Creator make all new yet forms like neighbouring Continent. This fact speaks volumes**. ... my theory explains this. But no other will.— **St. Helena** (**& flora of Galapagos?**) **same condition**." (Barrett et al. 1987:296). Clearly, Darwin's interest in the Galápagos plants was tied into his theory of evolution, which jelled after he read Malthus (1826) in September 1838, when he added natural selection to it.

On 21 November 1838, Henslow wrote again to Hooker that, "I shall leave at 13 Clements Green [his brother's house in London] the Galapagos plants, in my way thru Town tomorrow." [Porter 1980a:520]. A week later, Hooker wrote to Darwin that,

> Profr. Henslow has promised me your plants, but they have not arrived yet ....
> Your Gallapago Isld plants will be extremely interesting, there are a few in my fathers herbarium collected by the late David Douglas.... I hope that the plants will be as peculiar as those of St. Helena.... The ferns will perhaps form some key to the regions it may

> be most analogous to.. Professor Henslow has kindly promised to send your Galapago plants as well as the Antarctic.. I am not aware of any collector having been there but yourself & Douglas.. [Burkhardt and Smith 1986:411, 412]

The botanical collector David Douglas and ship's surgeon-naturalist John Scouler collected plants in the Galápagos in 1825, as did James McRae, collector for the Horticultural Society; the naturalist Hugh Cuming did so in 1829, but as indicated above, the first known Galápagos plant collector before Darwin was Archibald Menzies in 1795 (Porter 1980b).

Henslow again wrote to Hooker on 10 December 1843 that he would deliver the Galápagos specimens to him:

> I shall leave at 13 Clements Green the Galapagos plants, in my way thru Town tomorrow…. I had begun by a few random notes to examine them before I left Cambridge [for Hitchim in 1839] & have left them just as I inserted them at the time – Since I came here [Hitchim] I have had no time for them – always intending to recommence – but never being able to do so among my numerous engagements & duties – You will find an interesting set of plants – Pray publish them in any way you prefer. I am too happy to see justice done to Darwin's exertions to think of making any stipulations of any sort – Do just as you please – giving him due credit for collecting in a branch of science which formed no part of his studies, & solely to oblige me. [Porter 1980a:520–521]

Perhaps in confirmation of this last statement, in his next letter to Hooker (12 December 1843) Darwin writes, "From my entire ignorance of botany, I am sorry to say, that I cannot answer any of the questions, which you ask me.—" (Burkhardt and Smith, 1986:419). Hooker's latest letter (28 November 1843) was full of questions and comments on subantarctic plants; but Darwin does address some of Hooker's queries. He also adds:

> On the other hand, I hope the Galapagos plants (judging from Henslows remarks) will turn out more interesting than you expect.— Pray be careful to observe, if I ever mark the individual Isl^{d} of the Galapagos islands, for the reasons you will see in my Journal.— [Burkhardt and Smith 1986:420]

Darwin here refers to his observations on species distributions in the Galápagos in *Journal of Researches*. After discussing reptiles and birds, he turns to plants:

> I was also informed that many of the islands possess trees and plants which do not occur on the others. For instance, the berry-bearing tree [*Psidium galapageium* (Myrtaceae)], called Guyavita, which is common on James Island, certainly is not found on Charles Island, though appearing equally well fitted for it. Unfortunately, I was not aware of these facts till my collection was nearly completed: it never occurred to me, that the productions of islands only a few miles apart, and placed under the same physical conditions, would be dissimilar. I therefore did not attempt to make a series of specimens from the separate islands. It is the fate of every voyager, when he has just discovered what object in any place is more particularly worthy of his attention, to be hurried from it. [Darwin 1839b:474]

Hooker began his next letter to Darwin (12 December 1843–11 January 1844):

> The Galapagos plants are far more xtensive in number of species than I could have supposed, & are the foundation of an xcellent flora of that group: …. I was quite prepared to see the xtraordinary difference between the plants of the separate Islands from your journal, a most strange fact.. & one which quite overturns all our preconceived notions of species radiating from a centre & migrating to any xtent from one focus of greater development. [Burkhardt and Smith 1986:421]

Darwin begins his answer (11 January 1844), "I must write to thank you for your last letter; I to tell you how much all your views & facts interest me.—" (Burkhardt and Smith 1987:1). Two paragraphs mention Galápagos plants:

> Would you kindly observe one little fact for me, whether any species of plant, *peculiar* to any isl[d], as Galapagos, St. Helena or New Zealand, where there are no large quadrupeds, have hooked seeds,— such hooks as if observed here would be thought with justness to be adapted to catch into wool of animals.—
>
> Would you further oblige me some time by informing me (though I forget this will certainly occur in your Antarctic Flora) whether in isld like St. Helena, Galapagos, & New Zealand, the number of families & genera are large compared with the number of species, as happens in coral-isl[d], & as I *believe*? in the extreme Arctic land. … Do you suppose the fewness of species in proportion to number of large groups in *Coral-islets*, is owing to the chance of seeds from all orders, getting drifted to such new spots? as I have supposed [e. g., Darwin, 1839b:541].— [Burkhardt and Smith 1987:2]

These are subjects that Darwin pursued in depth in the 1850s, plant geography (e.g., Stauffer 1975:528–566) and plant dispersal mechanisms (e. g., Darwin 1857). This letter also contains his famous confession to Hooker that he believes that species are not immutable, that they evolve:

> Besides a general interest about the Southern lands, I have been now ever since my return engaged in a very presumptuous work & which I know no one individual who w[d] not say a very foolish one.— I was so struck with distribution of Galapagos organisms &c &c & with the character of the American fossil mammifers, &c &c that I determined to collect blindly every sort of fact, which c[d] bear any way on what are species.— … At last gleams of light have come, & I am almost convinced (quite contrary to opinion I started with) that species are not (it is like confessing a murder) immutable. … I think I have found out (here's presumption!) the simple way by which species become exquisitely adapted to various ends.— [Burkhardt and Smith 1987:2]

Darwin, of course, refers to the principle of natural selection, which, although it was also later revealed to a few others (Porter 1993), was not published until 14 years later (Darwin and Wallace 1858).

Hooker answers on 29 January 1844:

> That there was a beginning to the creation of plants on our globe is very true, we can hardly suppose that we have now only the remains of that original stock…. There may in my opinion have been a series of productions on different spots, & also a gradual change of species. I shall be delighted to hear how you think that this change may have taken place, as no presently conceived opinions satisfy me on the subject. [Burkhardt and Smith, 1987:7]

As with most of their correspondence at this time, there is much discussion of Patagonian and Fuegian plants and their distributions. Commenting on Darwin's above queries on dispersal mechanisms and plant geography, on 29 January 1844 Hooker wrote: "I am now examining the Galapago's plants & shall soon duly report to you on the state of the seeds as to arming, &c." and "Amongst these [Galápagos ferns] the number of genera to sp. is very large, as in all circumscribed portions of land." The letter ends: "You may depend upon my best exertions to name the Galapagos plants carefully: it is a slow business but I like it much.—" [Burkhardt and Smith 1987:6, 7]. Most of the large number of letters between Darwin and Hooker regarding the *Beagle* plant specimens from here through 1846 consist of queries and discussions of specific plants and their distri-

butions, so to keep the present paper from descending into minutiae, only subjects of greater importance to Darwin will be quoted and discussed hereafter.

In his next letter to Hooker (23 February 1844), Darwin writes:

> First for the Galapagos, you will see in my Journal [Darwin, 1839b] that the Birds, though peculiar species, have a most obvious S. American aspect: I have just ascertained the same thing holds good with the sea-shells.— Is it so with those plants, which are peculiar to this archipelago; you state that their numerical proportions are continental (is not this a curious fact?) but are they related in forms to S. America.— Do you know any other cases of an Archipelago, with the separate islands possessing distinct representative species?

Representative species are those that are "closely allied" (Darwin 1859:173). Darwin added:

> I fear my notes will hardly serve to distinguish much of the habitats of the Galapagos plants, but they may in some cases; most if not all of the green, leafy plants come from the summits of the islands, & the thin, brown leafless plants come from the lower arid parts: would you be so kind as to bear this remark in mind, when examining my collection. [Burkhardt and Smith 1987:10–11, 10]

Hooker answers Darwin's questions in his letter of 23 February–6 March 1844:

> The Flora of the Galapagos is most allied to that of the S. United States & to that of S. Brazil partially,.— … Though the Galapogean Flora is essentially S. American, the proportions of the Nat: Ords [modern families] to one another is remarkably different….
> With regard to the dissimilarity between the Flora of the several Islds of the group, that is too extraordinary a circumstance for me to offer any remarks upon, until the *florula* is drawn up, the further I proceed the more I wonder. …
> Enclosed is a list of as far as I have gone with the Galapagos Isld plants, whenever you return it I will add to it & send it again — I think I have it about 1/3 done, the proportion of new sp. is terrible among Dicot. & I must perpetrate one or two genera. [Burkhardt and Smith 1987:12, 13, 15]

In the event, Hooker described 75 new species and six new varieties (Hooker 1847a) and six new genera (Hooker 1846) of Dicotyledonae from the Galápagos based on Darwin's specimens. Hooker continued:

> It hardly appears, either that the genera are distributed equally through all the Isld^{s},— or that separate Isld^{s} have separate genera; untill however I have gone through the collection I shall forbear any more remarks, as I am often woefully out when applying the numerical test to my preconceived Ideas— [Burkhardt and Smith 1987:15]

Again regarding his collections, Darwin wrote to Hooker on 11 March 1844:

> I do not suppose I paid much attention to collecting the grasses at the Galapagos.— [He collected six of the then known 11 species (Hooker 1847a).]
> …With respect to the different isl^{d} having different species, the main point appears to me, whether any two or three islands have close *representative* species & another isl^{d} not having it is far less wonderful. … The tree Compositae [*Scalesia*; Darwin collected four of the then known six species (Hooker, 1847a).] were, I think, all, certainly most, from the summits of the Isl^{ds}: do not, pray, forget my question of the summits in these cases, having the most peculiar Flora.— [Burkhardt and Smith 1987:20]

On 31 March 1844, Darwin continued this discussion with Hooker:

> I have been exceedingly interested in the details about the Galapagos Isl^{ds}.— I need not say that I collected blindly & did not attempt to make complete series [as Henslow had taught him to do; see Kohn et al, 2005], but just took every thing in flower blindly.— The Flora of the summits & bases of the islands *appear* wholly different; it may aid you in observing, whether the different isl^{ds} have *representative species filling the same places in the economy of nature*, to know, that I collected plants from the *lower & dry region* in all the isl^{ds}. ie in Chatham, Charles, James & Albemarle (the least on the latter); & that I was able to ascend into the high & damp region only in James & Charles islands; & in the former I think I got every plant then in flower.— Please bear this in mind in comparing the representative species.— [Burkhardt and Smith 1987:23]

In his answer of 5 April 1844, a long one with much discussion of plant distributions throughout the world, Hooker wrote near the end: "I have worked the Galapagos Isld plants up to the Compositae & am now writing out clean the first part for printing." (Burkhardt and Smith 1987:27). But his Galápagos flora was not published until 1847.

On 1 June 1844, Darwin wrote to Hooker that, "I heard from Henslow some month or two ago, saying he had found a lot of Galapagos plants, which he had omitted to forward to you.— this must put your calculations out.—" (Burkhardt and Smith 1987:36). Darwin here uses "lot" in the sense of a parcel, not a considerable number. Henslow's letter to Darwin has not been found.

Over the following months, Darwin and Hooker exchanged a number of letters discussing plants, their geographical distributions, and the environmental features importantly affecting these distributions. The next known letter to discuss the Galápagos collections is from Hooker, dated 14 November 1844:

> My mother is copying out the 1st. century [i. e., first 100] of Gal. Isd. plants for L. Soc. [e. g., for Hooker, 1847a]. I did not tell you that I had to withhold it, from Henslowes sending me a supplement [see previous letter], which my *book* [Hooker, 1844–1847] prevented my working up. [Burkhardt and Smith 1987:83]

Hooker's next report, of 12 December 1844, was, "Galapagos Flora is progressing." (Burkhardt and Smith 1987:93). On 8 December, Hooker had visited Darwin at Down House, and the two of them had a long discussion on plants and their distributions. Darwin's notes on this discussion include the following comments: "Cocos Is^{d} (N. of Galapagos) has Mexican form of ferns — Galapagos allied to W. Indian Islands —, certainly American character flora, more than to continent. —" (Burkhardt and Smith 1987:399). These relationships of the Galápagos flora are repeated in Hooker (1847b). However, modern research shows that its main relationships are with adjacent South America (Porter 1984a; Tye and Francisco-Ortega, in press).

On 30 December 1844, Hooker writes another long botanical letter to Darwin that briefly mentions the Galápagos: "Galapagos flora goes on well, I have stuck at a highly curious new genus, amongst the supplements." (Burkhardt and Smith, 1987:104). This is probably *Pleuropetalum* (Amaranthaceae), which Hooker published independently from his other newly recognized Galápagos genera (Hooker 1846a). The next mention of the flora in their correspondence is in Darwin's letter to Hooker of 22 January 1845:

> I am delighted to hear of the Galapagos flora being done: would you, when it is printed in the Transactions give me a copy ... as you must have so many Botanical friends, to whom your papers wd be more valuable than to me, any old proof-sheet copy would do perfectly for me, & *any* such copy of any paper of yours, I shd be **truly** obliged for.— [Burkhardt and Smith 1987:127]

Hooker's letter announcing completion of (the first part of) his Galápagos flora has not been found. Later in his letter, Darwin stated: "… I am in a sort of negotiation with Murray, who wishes to get the power from Colburn & publish a 2d Edit:" (Burkhardt and Smith 1987:127). Henry Colburn was the publisher of *Journal of Researches* (Darwin 1839b), and John Murray became the publisher of the second edition (Darwin 1845), which benefited greatly from Hooker's examination of Darwin's plant specimens and Darwin's query to him of 16 April 1845:

> Did you make any comments criticisms or corrections on the margin of my Journal [Darwin, 1839b]; if so, will you kindly lend me your copy & never mind if any of your criticisms are severe or short & few. I shall have to shorten my Journal a little. [Burkhardt and Smith 1987:177]

Hooker also later read and commented on the proofs for Darwin.

Darwin wrote a number of letters to Murray regarding the second edition between 17 March and 2 September 1845, but Murray's answers have not been found. In what was probably the worst business decision he ever made, Darwin sold the copyright of the second edition of *Journal of Researches*, called *Voyage of the Beagle* since 1905, to Murray for £150. It was initially published in three parts, on 28 June, ca. 2 August, and ca, 30 August (Freeman 1977), and has been in print ever since.

On 16 April 1846, among other things, Darwin asked Hooker:

> Whenever an Abstract of your paper on the Galapagos plants appears, I hope you will try & get me a copy.—...
>
> I am determined not to give you much trouble or ask many questions now you are busy, but I must beg *sometime* for a single sentence about the Galapagos plants. viz. what percentage are (as far as is known) peculiar to the Archipelago? you have already told me that the plants have a S. American physionomy. And how far the collections bear out or contradict the notion of the different islands, having in some instances representative & different species. [Burkhardt and Smith 1987:177, 178]

On 28 April, he added: "I have been vexed at my stupidity in having mentioned the Galapagos Plants to you at this time, for my Journal comes out in three numbers & the Galapagos will be in the last." (Burkhardt and Smith 1987:182).

Hooker answered on the same day with a long letter, only part of which has survived:

> Either you have misunderstood me, or I have ill expressed myself about the Galapagos plants, it was only the *first part* that I had got ready, I however devoted 10 days uninterruptedly lately & finished the species of all the rest, except the *Leguminosae*, some 18, which Bentham will do. Said *first-part* has been 3 months before the L. Soc. But is not printed, when it is I shall not forget you. The proportion of new species is prodigious & even the old ones have been most difficult to name, as there are no floras of Mexico Peru & Chili, There are 185 species in all, a goodly number, (of flowering plants & 42 Cryptogamic). [Burkhardt and Smith 1987:183]

The included cryptogams were fungi, lichens, liverworts, mosses, and ferns. George Bentham, botanist at the Royal Botanic Gardens, Kew, was an expert on legumes. Hooker (1847a) acknowledges Bentham for assistance in identifying the 18 Fabaceae and Mimosaceae for him, However, all their six new species were described by Hooker, who in the letter lists numbers of species per island, endemic species, and those known from single islands. These and other comments are discussed in Hooker (1847a).

Darwin answered in his letter of May 1845 that, "I am very much obliged for your sketch of

the Galapagos flora; it really turns out a most interesting case: I shall be very anxious to hear the final result, when the Legum: are worked out.—" (Burkhardt and Smith 1987:185).

On 11–12 July 1845, Darwin wrote:

> I sh^{d} have written to you a few days ago, as I had some questions to ask & several points in your last letter [of 5 July], which I should much enjoy discussing with you: but on Wednesday an upsetting event happened in the fact of a Boy-Baby being born to us [George Howard Darwin]— may he turn out a Naturalist.
> ... First I have got a few questions about the Galapagos Plants, as I am now come (not in correcting press, but first time over) to that Chapter: I will put these questions on a separate paper & some of them you can answer by a word or two on the paper on its back & return it to me, pretty soon, if you can manage it. I cannot tell you how delighted & astonished I am at the results of your examination; how wonderfully they support my assertion on the differences in the animals of the different islands, about which I have always been fearful: I see that the case excites the interest of even R. Brown.— [Burkhardt and Smith 1987:216]

Robert Brown, as a member of the Council and Honorary Secretary of the Linnean Society, chaired the meeting of 4 March at which part of Hooker's "On the Botany of the Gallapagos Islands" was read (Anonymous, 1845). The sheet with Darwin's questions and Hooker's answers is appended to the letter. It is too long to repeat here. Darwin's last question was: "If the collection had been put into your hands: sh^{d} you have known that it came from the American quarter: w^{d} not Opuntia have told this? [cacti are only native to the Americas] would other genera have told the same story?" (Burkhardt and Smith 1987:219). On receiving this letter, Hooker answered (after 12 July) with his own full of information on Darwin's collections and the Galápagos flora, which Darwin used to advantage in the second edition of *Journal of Researches*. Toward the end of his letter, Hooker wrote:

> The collection is *out & out* S. American, & W. coast, but from the peculiarity of some genera & most species, I should not have known where to put it, supposing Galapagos not to xist. I know so much of the Flora of the coast as not to expect so much novelty from any 100 miles of it, if forced to assign the place it w^{d}. probably be Panama ... The Flora is S. American throughout in character. [Burkhardt and Smith 1987:222]

At that time, Panama was part of Colombia and was considered, therefore, to be part of South America. In a second letter sent about the same time (mid-July 1845), Hooker sent detailed information about plant distributions in a number of other islands and elsewhere.

Darwin's next letter, of 22 July–19 August 1845, acknowledges receipt of Hooker's last letter and asks,

> And now for the main object of my letter; it is to ask, whether you would just run your eye over the proof of my Galapagos Chapter, where I mention the plants, to see that I have made no blunders or spelt any of the scientific names wrongly. ...
> Farewell, my dear Hooker with many thanks for your long letter, always most interesting to me. [Burkhardt and Smith 1987:226–227]

Darwin wrote again (15 or 22 August 1845):

> I enclose the proofs; would you please look over the whole of the Galapagos Ch. As the vegetation is incidentally mentioned in two or three places; you can skip about the tortoises & lizards, tameness of birds which is as before; all the rest is much altered.— I have tried to make it as little purely scientific as possible— I hope there are no material errors

> in the Botany part: the proofs have been revised once, but I have not time to look them over again before sending to you.— W[d]. You please return them soon, as the Press waits for them.— [Burkhardt and Smith 1987:237]

Presumably, Hooker read and commented on the proofs, then returned them to Darwin. However, neither the marked proofs, nor a covering letter from Hooker, have been found.

Darwin and Hooker continued to correspond about the *Beagle* collections, species distribution, and the nature and origin of species. They also occasionally discussed Galápagos species until the publication of Hooker's papers on the flora (1847a) and phytogeography (1847b) of the islands.

Upon reading the manuscript of Hooker's paper on the geographical distribution of Galápagos plants, Darwin wrote to him (23 November 1846):

> I have read your paper pretty carefully, but to fully appreciate it, it ought to be read two or three times, & that I shall do when in print. In my opinion, it is without comparison, the best essay on geograph. distrib. in any class, which I have ever met with; & poor judge though I may be, I have looked far & wide for such discussions in vain. I will praise it no more, though in truth I could say with earnestness much more.— [Burkhardt and Smith 1987:369]

Several pages of "small criticisms" follow. Hooker answers (24 November 1846): "Ten thousand thanks my dear Darwin for the most ungracious of all offices executed & in the most gracious manner. I do not think we have much to quarrel about." (Burkhardt and Smith 1987:371). Hooker's pioneer vegetational and phytogeographic study of the Galápagos Islands (Hooker 1847b), like his Galápagos flora (Hooker 1847a), was based primarily on Darwin's collections.

There have been misinterpretations in the dating of Hooker's flora and his vegetational and phytogeographic study (Porter 1980b). The flora paper was read at three meetings of the Linnean Society of London on 4 March, 6 May, and 16 December 1845. A summary was published in 1846 (Hooker 1846). This summary is often cited as having been published in 1849, but this is the year that the completed volume of *The Transactions of the Linnean Society* was published. The fascicle containing the summary is dated 1846. Likewise, the flora is often cited as being published in 1851, but the fascicle containing it is dated 1847. The vegetational and phytogeographic paper was read at the Linnean Society on 1 and 15 December 1846, and a summary was published in 1847 (Hooker 1847c). These are often cited as being published in 1851 and 1849 respectively, but the fascicles containing them are both dated 1847. Printed fascicles of the Linnean Society's journals were made available to members as they were published.

Conclusion

From the data given in the section above devoted to the localities where Darwin collected, it can be calculated that he gathered 756 different species, subspecies, or varieties of vascular plants on the *Beagle* voyage. They are referred to as species throughout this paper because they have bounced from one category to another over the years. Of the 902 collections, 220 (24%) were described as new. This is an astonishing number, which reveals how poorly known were the floras of those places visited, especially the Galápagos Islands. The new taxa are represented by 440 type specimens, which include holotypes, isotypes, syntypes, paratypes, lectotypes, isolectotypes, and paralectotypes. Species with Darwin's collecting numbers were 66, only 9% of the total. Again, this is an astonishing amount, apparently showing that Darwin found few collections of sufficient interest to number. On the other hand, it may just indicate that he did not have sufficient time to deal promptly with the plants because of the many geology and zoology specimens he also had collect-

ed. Finally, the collections are on 1,476 herbarium sheets; the sheets at Cambridge carry about 2,700 specimens (Darwin's Plants from the *Beagle* Voyage, 2009).

Many uninformed people today think of Darwin only as a zoologist. However, as one looks at his scientific career, it clearly can be seen that he was successively a geologist, then a zoologist, and finally a botanist. He began his first landfall on the *Beagle* voyage, in the Cape Verde Islands, by collecting and observing rocks, animals, and plants, His interests also were in this order, as can be seen by his geology notes covering 1,383 pages, his zoology notes 368, and there being no separate botany notes, although about 20% of the pages in his Zoology Diary are devoted to descriptions of plants or vegetation (Porter 1986). In spite of his obvious interest in plants on the voyage, and his homage to Henslow as his botanical mentor, it must be remembered that he wrote to Henslow early in the journey (18 May 1832) from Rio de Janeiro that, "Geology & the invertebrate animals will be my chief object of pursuit through the whole voyage.—" (Burkhardt and Smith 1985:237).

Charles Darwin will forever be remembered for the *Beagle* voyage, the Galápagos Islands, and the ill-named Darwin's finches. The latter were not given this name until 1935 and are best called Galápagos finches. It is a myth that they played a role in Darwin's ideas on evolution while he was in the archipelago (Sulloway 1982). Nevertheless, I hope that the foregoing essay will have shown the reader that a visit to these islands following months spent in Chile made him aware of the importance of the biogeographical relationships of their floras and faunas. His comments in his diary and to Henslow and Hooker on "centers of creation" before and while on the islands and after his voyage give strong hints of his resolute interest in organic evolution. This interest is demonstrated by Darwin's observations on fossils, animals, and plants found throughout his letters, manuscripts, and notebooks at this time, culminating in the first sentence of *On the Origin of Species*: "When on board H.M.S. 'Beagle,' as naturalist, I was much struck with certain facts in the distribution of the inhabitants of South America, and in the geological relations of the present to the past inhabitants of that continent." (Darwin 1859:1). This was especially true from the living and fossil mammals of Patagonia, and the plants and animals of the Galápagos Islands and adjacent South America. They were the keys to his discovery of the Principle of Natural Selection.

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Darwin, Barnacles and the Galápagos: a View Through a 21st Century Lens

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Darwin's discovery and collection of the acrothoracican barnacle, that he referred to in correspondence as "Mr Arthrobalanus", from Patagonia in 1835 instigated an intense study of barnacles for close to a decade and the publication of four monographs over a period of four years (1851-1855).

Darwin's visit to the Galápagos in 1835 pre-dated his focused studies on barnacle evolution by over a decade. Therefore, he paid little attention to barnacles on the Galápagos. He did collect some barnacles in the Galápagos, but these specimens were apparently lost. Therefore he had to ask other scientists to collect material for him when he began his Cirripedia work in 1846. He also studied the collections at the British Museum and borrowed material from the Museum National d'Histoire Naturelle in Paris.

Darwin's four landmark monographs of Cirripedia forged the first major modern comparative morphological study of that group. These works are still in use by barnacle biologists today, though mostly as a reference to early recognition of various morphological characteristics and name usage.

Current tools and techniques such as phylogenetics, scanning electron microscopy and molecular-level comparisons have allowed present day cirripedologists to delve more deeply into the taxonomy and systematics of the group. We now realize that although Darwin recognized many of the genus and subgenus level clades, he could not prove the stability of some morphological characters and he failed to determine many closely related and cryptic species, which we are still in the process of discovering.

Examples from the Galápagos include the recognition of a morphologically cryptic, but genetically distinct, new species in the genus *Conopea*. As recently as 1986, taxonomic study cited intra-specific morphological variability in a widespread eastern tropical Pacific species of *Megabalanus*, following Darwin's view of morphological variation within barnacle species. However, a genetic break between populations of *Megabalanus peninsularis* from Baja California and the Galápagos/Panama area suggests another, more recently diverged, cryptic species pair.

The Salton Sea population of *Amphibalanus amphitrite* provides examples of both the intra-specific morphological variation that Darwin cited in his monographs and a great accumulation of shell material that illustrates his statement that "These Cirripedes now abound so under every zone, all over the world, that the present period will hereafter apparently have as good a claim to be called the age of Cirripedes, as the Palaeozoic period has to be called the age of Trilobites."

As in Darwin's time, barnacles continue to be an excellent taxon for the study of evolution: with an extensive fossil record, adaptations to extreme physical environments and host-specific symbioses with many types of organisms.

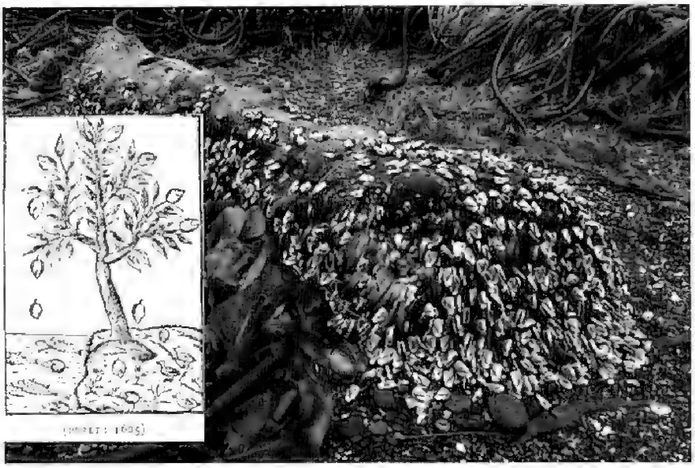


FIGURE 1. The "barnacle tree" illustration of Duret 1605 (left) and the real-life inspiration, a drift log washed ashore with attached *Lepas anatifera*.

Charles Darwin became fully engaged with barnacle research as the result of his interest in a miniscule, atypical burrowing form nestled in pits made in a shell of the muricid snail *Concholepas concholepas* that he discovered in Patagonia in 1835 during the HMS "Beagle" voyage of discovery. Darwin was only 22 years old when that voyage began in 1831 and 27 when it terminated in 1836. It was not the voyage's most famous stop, from 15 September to 20 October 1835, to survey briefly the Galápagos Islands region that led him to study barnacles intensely for close to a decade and produce four monographs (Darwin 1851a, 1852, 1854a, 1855). Rather, it was the collection of the tiny Patagonian acrothoracican barnacle that he referred to in correspondence as "Mr Arthrobalanus".

Prior to, and during, his barnacle study years, Darwin often mentioned his "species work" to colleagues and confidants. The first glimmer of these ideas came to light in 1837 in his sketch of a branching tree with a notation "I think". Later, in correspondence with Joseph Dalton Hooker in 1842 Darwin refers to his "species work". The full spectrum of Darwin's ideas on speciation and natural selection, variation in physical characteristics leading to differential success in survival and reproduction that leads to the inheritance of the most advantageous traits in offspring, was obviously percolating through his mind while he studied and wrote about barnacle taxonomy.

Darwin's five week-long visit to the Galápagos in 1835 pre-dated his studies for the monographic works on barnacle evolution (begun in 1846) by over a decade. He did collect some barnacles in the Galápagos, but these specimens were apparently lost; therefore, he had to ask other scientists to collect study material for him. He also used the collections at the British Museum and borrowed material from the Museum National d'Histoire Naturelle in Paris. John Edward Gray, a barnacle biologist at the British Museum, helped with access to collections and suggested to Darwin that he monograph the barnacles.

His four landmark monographs of Cirripedia, published from 1851–1855, forged the first major modern comparative morphological study of that group. Impressively, there was little previous work of consequence by others upon which to build. Although it had been over two hundred years since naturalists of the early 1600s had observed "Barnacle trees", drift logs covered with barnacles with long fleshy stalks that resembled goose necks to the Renaissance naturalist and suggested that "goose barnacles" were larval forms of "barnacle geese" (Fig. 1), not a lot of progress had been made in the study of barnacle biology. Nearly all biologists thought that the calcareous shell of barnacles placed them among the Mollusca until 1830 when J.V. Thompson discovered the naupliar larvae of barnacles, a form shared with all other crustaceans, not mollusks. In spite of this advance, old concepts of the taxonomy of Cirripedia hung on and by 1834 Cuvier and others still considered the "Cirrhopoda" as a 6th class of Mollusca.

Compared to previous efforts, Darwin's studies were highly rigorous and thorough. Michael Ghiselin referred to his detailed study of barnacles from every possible vantage point as the begin-

ning of the "Darwinian method" of scientific study (Ghiselin 1969). Critical to these detailed observations were his new microscope technology and his great skill at making study slides. He used it in making detailed anatomical studies of various life stages, including metamorphosis from larva to adult.

One of the enduring legacies of Darwin's monographs is the nomenclature that he developed and standardized for various structures. Some of these terms he modified from previous works, but for the most part he coined new names. In the introductory remarks of the second monograph he modestly wrote: "I have unwillingly found it indispensable to give names to several valves, and to some few of the softer parts of Cirripedes." and "The names which I have imposed will, I hope, be thus acquired without much difficulty." (Darwin 1852:3).

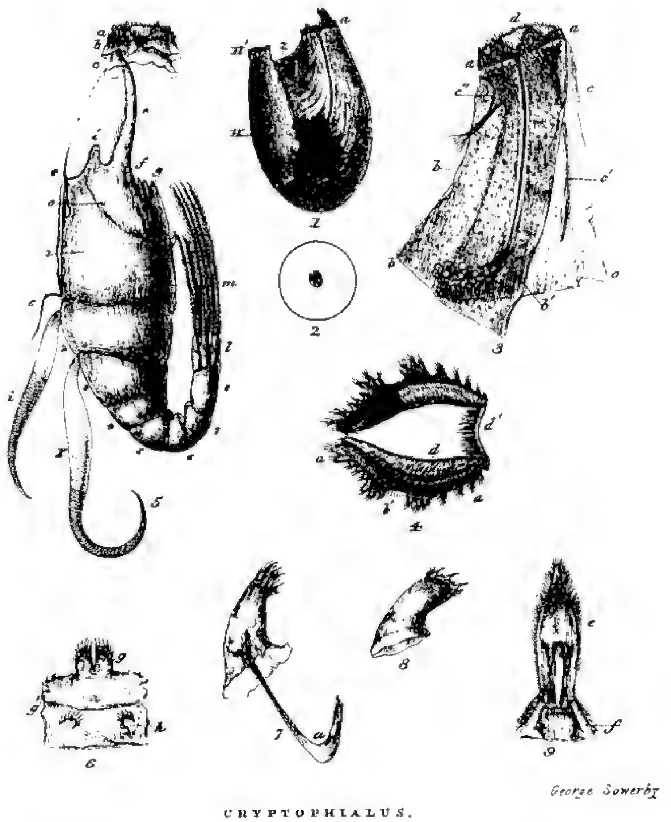


FIGURE 2. Hooker's drawings of "Mr Arthrobalanus", *Cryptophialus minutus*, as they appeared in Darwin's (1854a) monograph. Note the circled figure "2" on the plate, a "life-sized" illustration.

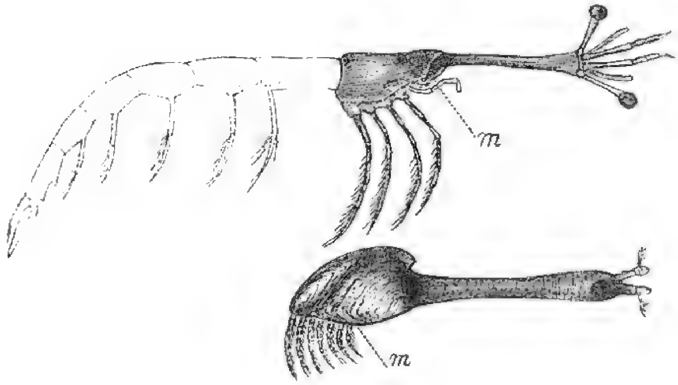
He also discovered and named dwarf and complemental males and developed the anatomical nomenclature in use today. This body of work in four volumes forms the framework of our modern classification of Cirripedia. To his great consternation, he did make some errors in anatomical interpretations that were quickly noted and corrected by contemporaries. It was difficult for him to admit his errors and come to terms with it as he was convinced that his careful study could not help but lead to proper assessment of various structures (see Newmann 1993:369, for examples).

The tiny burrowing cirripede that Darwin called "Mr Arthrobalanus" in some of his correspondence was eventually named *Cryptophialus minutus*, when he published the description as part of his monograph on living balanids (Darwin 1854). It is ironic that the animal that launched his studies on Cirripedia was the next to the last described species in his four monographs, appearing on page 566 (of 605 descriptive pages) of his final publication on barnacles.

Here he noted "I am greatly indebted to Dr. [J.D.] Hooker, for having several years ago, when I examined this my first cirripede, aided me in many ways, and shown me how to dissect the more difficult parts, and for having made for me several very correct drawings, which, with some subsequent alterations [by George Sowerby], are now engraved." Hooker's drawings were finally published with Darwin's description of *C. minutus* (Fig. 2). The circled figure labeled "2" in the published plate depicts the life size of *Cryptophialus minutus*, a few millimeters in diameter.

Darwin also found inspiration in the work of Henri Milne-Edwards on embryological homol-

ogy and archetypal crustacean concepts. He brought these ideas to an archetypal cirripede concept, taking the ground-plan of what Darwin called a "Stomapod Crustacean" from Milne Edwards' drawing of *Leucifer*, a sergestid decapod crustacean, and drawing homologies with basic lepadomorph cirripede anatomy (Darwin 1854, p. 28; Fig. 3 herein).



[m.—Mouth.]

FIGURE 3. Milne-Edwards' sketch of *Leucifer* (top) interpreted and homologized with a modified *Lepas* (below), highlighting the homologies of major external parts: reduction of the abdomen in Lepas, position of the thoracic limbs and mouth. The antennae and eyes are not present in adult *Lepas*, but were added by Darwin to indicate the anterior most end.

Vital to Darwin's anatomical studies of Cirripedia was the microscope built by Smith and marketed at the time as the "Darwin microscope". This instrument magnifies about 1300X. But Darwin probably used this advance in reflected light technology to work from about 100x to 800x magnification range. This instrument was a great improvement on the microscope Darwin used on the HMS "Beagle", with which he first observed specimens of "Mr Arthrobalanus" in Patagonia.

Clearly, today's microscopes and imaging equipment are far superior to the technology existing in Darwin's time. Scanning electron microscopes (SEM) and optical digital imaging equipment allow us to see details of structures that Darwin could not. These observed details are also more easily illustrated in publication and shared with other scientists. Darwin dealt with professional illustrators working painstakingly to create woodcut images that were transferred onto paper with mixed results. Newman (1993) details the frustration of Darwin with the poor quality of some of these woodcut images in his monographs. Modern scientists take digital images from light or electron microscopes and the same day send electronic files of those images to colleagues around the world via the internet.

Darwin's "varieties" explored: morphological plasticity, stability and cryptic species

The "species work" had a profound influence on his views of intraspecific variation that biased his work on barnacles (Newman 1993). Newman (1993) notes that Darwin needed species that varied in morphology, as variation in form within a species allows selection to occur and drive speciation. Darwin often concluded that highly variable barnacle species are broadly, even globally, distributed. He described several species as wide-spread taxa with many morphological "varieties" that he characterized and illustrated in his monographs.

Two of these highly diverse "species" of Darwin's that contribute to the Galápagos fauna are his *Balanus tintinnabulum* (11 Darwin varieties, now in the genus *Megabalanus*), and *Balanus amphitrite* (9 Darwin varieties, now in the genus *Amphibalanus*). Darwin (1854:155) lamented, "I must express my deliberate conviction that it is hopeless to find in any species, *which has a wide range, and of which numerous specimens from different districts* are presented for examination, any one part or organ…absolutely invariable in form or structure" [italics Darwin's, for emphasis]. Further, the inability to distinguish what he could consider stable characteristics for the populations

within his species led him to state, "I will only add, that after studying such varying forms as B. tintinnabulum and amphitrite it is difficult to avoid, in utter despair, doubting whether there be such a thing as a distinct species, or at least more than a half a dozen distinct species, in the whole genus Balanus." (Darwin 1854:243).

In addition, in his 1854 monograph on living sessile barnacles the genus *Balanus* has six "section" groupings within it. These "section" groupings are now generally accepted as genera-level taxa; many "varieties" are accepted as species. Conversely, several of Darwin's varieties are now thought to be synonymous with previously described species. It is understandable that Darwin would not have known about all previous descriptions as many were cursory and not widely available publications. Of course, modern scientists have the advantage of a large and well reviewed literature available as electronic on-line versions or paper copies from their colleagues, journals and libraries.

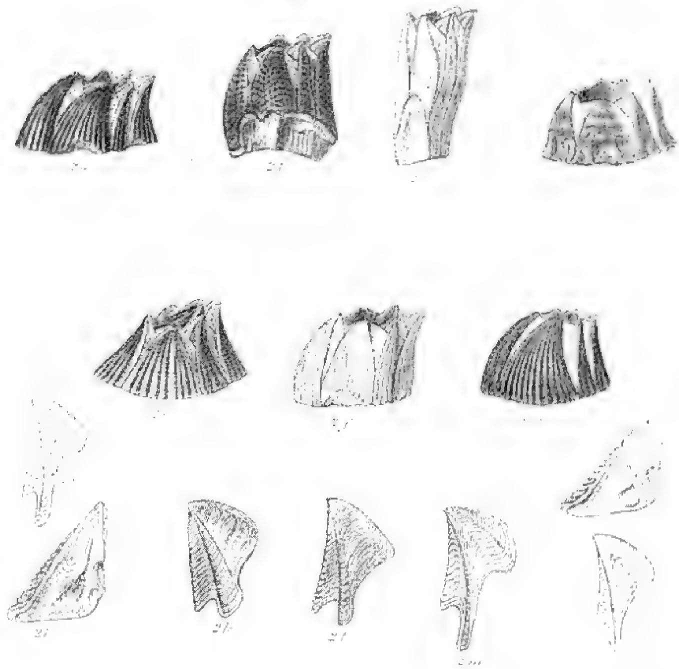


FIGURE 4. Darwin's "*Balanus amphitrite*" varieties (1854a; Plate 5, caption on p. 643).

Species distribution patterns are much clearer now than in Darwin's time. With our current knowledge of plate tectonics, oceanic currents, island evolution and larval dispersal, biogeographic patterns of species are more obvious, as well as better understood and interpreted. Only the barnacle species adapted to fouling other organisms, flotsam or human structures and vessels are considered truly cosmopolitan.

The "Balanus amphitrite group" of Darwin is a somewhat confusing mixture of morphologically variable, nearly cosmopolitan, fouling species and morphologically distinct taxa that have been diagnosed with species or genus-level characteristics, all within the subfamily Amphibalaninae (Pitombo 2004). One can certainly understand Darwin's frustration with the taxonomy of this group. Of the nine morphological "varieties" Darwin described in his "Balanus amphitrite group", five (*Amphibalanus amphitrite*, *A. improvisus*, *A. variegatus*, *A. venustus* and *Fistulobalanus pallidus*) are now recognized as distinct species (Henry and McLaughlin 1975; Pitombo 2004). *Amphibalanus amphitrite*, *A. improvisus*, *A. venustus* and *F. pallidus* have spread world-wide throughout tropical and sub-tropical seas as fouling species on ships or through other human activities such as aquaculture of oysters. *Amphibalanus variegatus* has a somewhat more circumscribed range in the western Pacific and Indian Oceans.

Darwin (1854; Plate 5, Fig. 2, caption on p. 643) had George Sowerby illustrate what he considered variants of a single species, "*Balanus amphitrite*" (Fig. 4, herein). In his woodcut plate, the specimen figures labeled as 2a, 2d, 2e-g are conical or nearly conical in shape, with only very small contact areas with other individuals visible in 2a and 2f. The individual illustrated in 2b is nearly

cylindrical with contact areas with other individuals over much of the basal half of the wall. The specimen figured in 2c is tulipiform with contact areas along the entire basal margin, extending nearly halfway up the shell wall, indicating very crowded growth. The plate also illustrates the extreme variation in terga form (2k-o) in Darwin's variants of "*Balanus amphitrite*".

Evidence for morphological "variation": morphological plasticity in *Amphibalanus amphitrite*: a Salton Sea experiment

The challenge facing Darwin with the amphitrite group is clearly visible in the morphological plasticity exhibited by *A. amphitrite*. Rogers (1949) first noted that *A. amphitrite* from Salton Sea were morphologically distinct from those individuals living in the bays along the southern California coast. He followed Darwin's convention of describing a new "variety" or subspecies for the Salton Sea population, naming it *Balanus amphitrite saltonensis*. The fact that the Salton Sea population was initially established in 1941 from individuals attached to a mooring buoy moved from San Diego harbor, suggests that the individuals are morphologically plastic rather than fixed for the different shell wall shape (cylindrical vs. conical) and opercular plate morphology. To test this hypothesis Van Syoc (1992) performed a transplant experiment, moving newly settled barnacles from the Salton Sea to Mission Bay, San Diego, California and removing individuals as they grew to avoid any contact of shell walls of adjacent individuals.

FIGURE 5. Lynn Newman standing on the barnacle shell covered shore of the Salton Sea. In her hand, she holds some of the shells of *Amphibalanus amphitrite* that cover the beach to a depth of a meter or more in places. (Photo by W.A. Newman, with permission.)

Barnacle shells and opercular plates from the transplanted individuals developed the morphological characteristics commonly observed in the well-spaced growing conditions of the coastal harbor forms (conical shell wall, well-calcified terga with broad spurs), not those found in the dense Salton Sea population where all individuals grow in shell wall contact with others (cylindrical or tulipiform shell wall, lightly calcified terga with narrow spurs) (Fig. 5 and 6).

The highly crowded conditions of the Salton Sea habitat lead to the light calcification of opercular plates and the extended vertical, rather than horizontal, growth of the shell wall plates. These extreme circumstances are rarely found in nature, but examples do exist in areas subject to flooding by rare tidal or storm events in river mouths or dry lake beds adjacent to estuaries. The Laguna Salada at the head of the Gulf of California (Van Syoc 1992) and the Mio-Pliocene Bouse Formation fossil coquina in banks of the Colorado River delta (Zullo and Buising 1989) are Recent and fossil examples, respectively, of this condition.

Cryptic species: Modern taxonomic tools sort out morphologically similar taxa

Recent advances in molecular-level phylogenetics are providing scientists with the tools to distinguish species that were previously taxonomically difficult due to seemingly intra-specific mor-

phological variation or morphologically similar or identical geographically separate populations. These cryptic species are often buried within Darwin's taxonomy of what he considered variable species. One example is the *Megabalanus tintinnabulum* (formerly *Balanus tintinnabulum*) group. Darwin (1854) redescribed *Balanus tintinnabulum* (of Linnaeus) as a variable species with 11 named varieties from around the world in tropical seas. Subsequently, Pilsbry (1916) named two geographically disjunct subspecies *B. tintinnabulum galapaganus* (Galápagos) and *B. tintinnabulum peninsularis* (Cabo San Lucas, Baja California). More recently, Henry and McLaughlin (1986) synonymized *Megabalanus galapaganus* with *M. peninsularis* claiming it to be a morphologically variable species, ala Darwin, with a range from the Galápagos and South America mainland, north to Baja California, Mexico.

To test Henry and McLaughlin's claim, DNA sequences from fragments of the mitochondrial gene cytochrome c oxidase subunit one (CO1) gene of animals from Isla Isabela and Isla Wolf in the Galápagos, the Pacific coast of Panama, and the Baja California, Mexico were analyzed. Preliminary data from this analysis provide some evidence of distinct genetic breaks between southern *Megabalanus* populations from the Galápagos, mainland Ecuador, and Panama and northern populations from Baja California (Fig. 7).

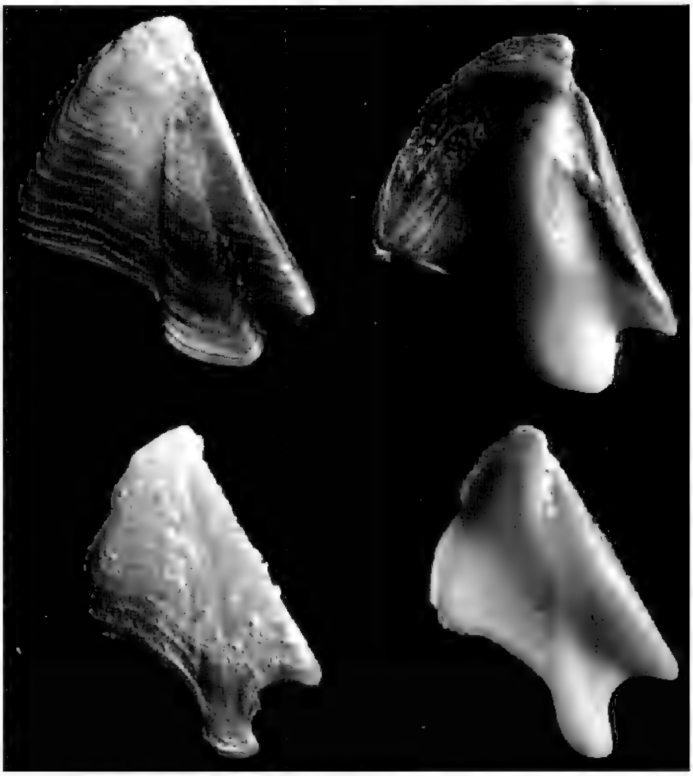


FIGURE 6. Terga from *Amphibalanus amphitrite* from the Salton Sea (lower terga) and those grown from newly settled Salton Sea individuals in uncrowded conditions on glass plates in Mission Bay (top terga).

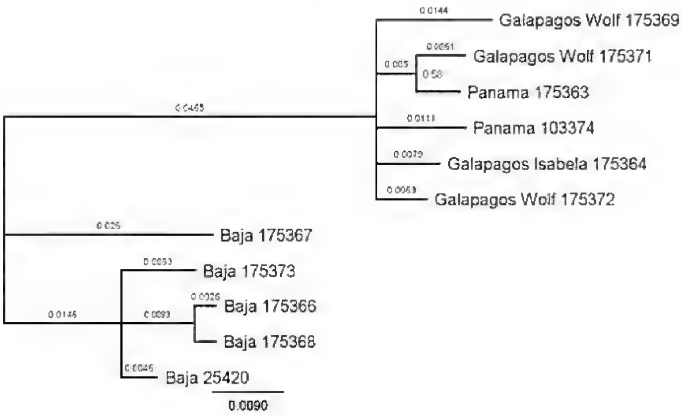


FIGURE 7. Bayesian analysis (Mr. Bayes, Huelsenbeck and Ronquist 2001) of CO1 sequences for specimens from the Galápagos, the Pacific coast of Panama, and Baja California, produces a tree with two clades. One clade contains sequences derived from the Baja California animals and the other of the Galápagos and Panama samples. The genetic distance between the two clades is 0.034 (or 3.4%) with a net distance between the two groups of 0.024 (or 2.4%) with a standard error of 0.006 (or 0.6%) as calculated using MEGA 4 (Tamura et al. 2007). Individual branch tips are labeled with the CASIZ catalog number as well as the geographic region of origin.

Additional sequences from individuals from Central America and southern Mexico would help further clarify the phylogeography and genetic diversity of these populations. It is possible that the two distinct clades in the present data set will blend into a latitudinal cline if haplotypes from individuals in southern Mexico and Central America fall between these two clades. However, the net genetic distance of about 2.4% between clades is more than generally expected from intra-specific variation.

Larval forms disperse further or shorter distances depending upon ocean currents and other sea conditions. Temperature is a proxy that allows us to visualize these changes that can occur within a few years. These changes can be dramatic and create bottlenecks and local extinctions. Examination of the persistent tropical eastern Pacific sea surface temperature as well as intermittent El Niño oceanographic conditions suggest that there may be a thermal barrier to dispersal across coastal Central America between Panama and Mexico (Fig. 8). Note the two warm pools off the coast of Central America that could prevent successful dispersal to the north and south. This phylogeographic pattern is similar to that found for other shallow water, coastal barnacles in the tropical eastern Pacific (e.g. Van Syoc 1994, *Pollicipes elegans*; Wares et al. 2009, *Chthamalus spp.*).

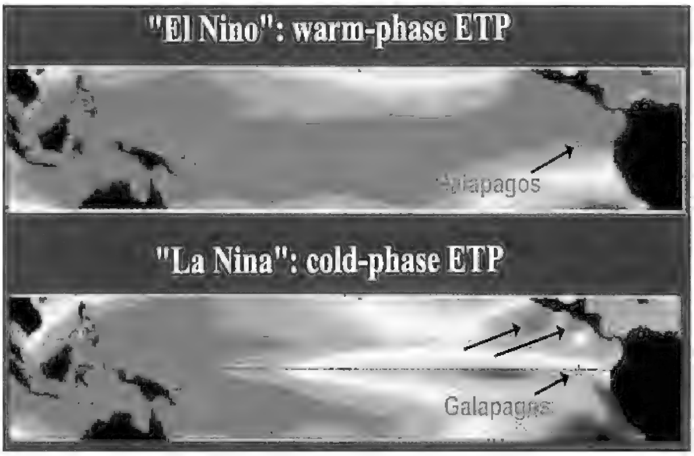


FIGURE 8. The position of the Galápagos Islands in reference to sea surface temperatures during El Niño and La Niña phases. Persistant coastal thermal barriers (arrows) exist in southern Mexico and northern Central America during the "cool phase" in the ETP.

Another "wide-spread" species fragments into several distinct taxa under greater scrutiny

Conopea galeata is a Linnean species (originally described as *Balanus galeatus*) re-described by Darwin (1854) from specimens collected on the Atlantic coast of the southeastern U.S. and the Caribbean. Subsequently the name has been attached to populations as distant as the Eastern Pacific, from California to the Galápagos, and the Philippines (see Newman and Ross 1976 for summary of biogeography and references). The identification of *Conopea* broadly geographically distinct populations from the Philippines, Galápagos and Caribbean as *Conopea galeata* in spite of morphological variations, may be due to the authority of Darwin's lingering shadow over barnacle taxonomy.

Turning again to molecular-level evidence, we find individuals from the *Conopea sp.* population identified as *Conopea galeata* by Zullo (1966) in the Galápagos are over 19% divergent in CO1 sequence from the Caribbean coast of Panama *Conopea galeata* population (D. Carrison, unpubl). When a DNA sequence divergence of this magnitude is taken into consideration, the slight, but noticeable, differences in morphology of opercular plates of the Caribbean and Galápagos samples can be viewed by the taxonomist as viable differences between species-level taxa and not intra-specific geographic variation as postulated by Darwin and continued by subsequent bar-

nacle taxonomists. The name *Conopea galeata* should be applied only to the Caribbean and western Atlantic populations.

Conclusions

Barnacles remain model organisms for study of evolution for many of the same reasons Darwin cited. They have an extensive, world-wide fossil record. Their shells can accumulate in great masses, as evidenced by the Salton Sea barnacle shell beaches and the Bouse Formation coquina in the Colorado River Delta. Barnacles have evolved various adaptations to extreme physical environments and host specific symbioses with many types of organisms.

This truly is the Age of Barnacles. "These Cirripedes now abound so under every zone, all over the world, that the present period will hereafter apparently have as good a claim to be called the age of Cirripedes, as the Palaeozoic period has to be called the age of Trilobites." Darwin (1851.)

Darwin's struggle to differentiate intra-specific variation from inter-specific variation continues and even with modern tools there are uncertainties. However, it is clear that many of Darwin's described varieties are distinct species and that his concept of wide-spread and highly variable species is, for the most part, no longer valid.

As in Darwin's day, museum collections continue to play an important role in preserving historical studies and allowing a glimpse back in time. They were critical to Darwin's barnacle studies and continue to serve an important function, especially as we develop molecular-level tools to study taxonomy and evolution.

Acknowledgements

Bill Newman's insightful review of Darwin's barnacle work served as the primary inspiration for this contribution and I thank him for his mentorship over many years. Michael Ghiselin invited me to present this work as a lecture at the Galápagos Symposium of the 2009 AAAS Pacific Division meeting at the California Academy of Sciences in San Francisco. John McCosker included me in the CAS Galápagos Expedition of 1994, when many of the specimens used for the genetic and morphological analysis were collected. Dana Carrison provided the *Conopea* DNA sequence data from her on-going thesis research on Atlantic, Caribbean and eastern Pacific *Conopea* populations. Christina Piotrowski and Kristen Roberts derived the *Megabalanus* DNA sequence data.

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The Fishes of the Galápagos Archipelago: An Update[1]

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The inshore fishes of the Galápagos archipelago provide zoogeographers and ichthyologists with an opportunity to study the evolution and endemism of nearshore tropical eastern Pacific reef fishes. We report upon recent discoveries made using the untethered submersibles *Johnson-Sea-Link* (to 1000 m depth) at the Galápagos and the *Deep-See* (to 500 m depth) at Cocos Island, Costa Rica. The history of ichthyological exploration at Galápagos is reviewed and the oceanographic environment is described. We update previous reviews of the Galápagos ichthyofauna and list the 550 shorefishes representing 128 families (within 50 km from shore, not including mesopelagic species) now known from the archipelago. The faunal composition is summarized as follows: 44.8% are shared with the Panamic fauna; 5.8% are shared with Peru and/or Chile; 15.6% are cosmopolitan; 16.1% are shared with the Indo-Pacific (approximately 14 species are non-established vagrants); 13.6% are endemic to the Galápagos; and 17.8% are endemic to the Galápagos and Cocos and/or Malpelo islands. Patterns of Galápagos and Galápagos/Cocos Island endemism are discussed. Endemism of Galápagos fishes living between 200-1000 m exists but due to data limitations can only be approximated. We provide the first color photographs of *Myroconger nigrodentatus*, *Liopropoma longilepis*, *Serranus aequidens*, *Serranus stilbostigma*, and *Hoplostethus pacificus*. New records of Galápagos fishes include: *Chimaera* sp., *Hydrolagus* sp., *Apristurus* sp., *Bythaelurus* sp., *Galeus* sp., *Echinorhinus cookei*, *Dasyatis* sp., *Torpedo peruana*, *Myroconger nigrodentatus*, *Echidna nebulosa*, *Gymnothorax angusticeps*, *Bathycongrus* sp., "*Ophisoma*" sp., *Argentina aliceae*, *Physiculus nematopus*, *Monomitopus malispinosus*, *Phenacoscorpius* sp., *Pontinus vaughani*, *Pontinus* spp. (3 undescribed species), *Scorpaenodes rubrivinctus*, *Liopropoma longilepis*, *Serranus aequidens*, *Lutjanus guttatus*, *Pristipomoides zonatus*, *Chaetodon unimaculatus*, *Halichoeres adustus*, *Halichoeres melanotis*, *Entomacrodus chiostictus*, *Sphyraena barracuda*, *Benthodesmus tenuis*, *Hippoglossina bollmani*?, *Monolene maculipinna*, and *Arothron nigropunctatus*?. New records of Cocos Island fishes include: *Myroconger nigrodentatus*, *Echinorhinus cookei*, *Gymnothorax angusticeps*, *Liopropoma longilepis*, and *Halichoeres raisneri*. *Halichoeres raisneri* is also reported for the first time from Malpelo Island. *Leptocephalus alternatus* Fowler 1938 is synonymized with *Quassiremus evionthas* (Jordan & Bollman 1890). Previous records of *Chaunax latipunctatus*, *Hypoplectrodes semicinctus* and *Lactoria diaphana* from Galápagos are found to be invalid. The status of *Azurina eupalama*, not seen alive in Galápagos since the 1982/1983 ENSO event, is discussed.

[1] The results of this study were first presented at the 90th annual meeting of the AAAS, Pacific Division, Darwin and the Galápagos symposium on 15 August 2009.

Introduction

The Galápagos Islands have long been noted as a natural laboratory for studies of isolation and evolution of terrestrial and marine organisms. Charles Darwin, a keen naturalist and avid angler (Pauley 2004), made the first collection of fishes, and since that time ichthyologists have made numerous and fascinating discoveries at that island laboratory. Published listings and treatments of the Galápagos ichthyofauna began with Jenyns (1840-1842) (Figs. 1-2), followed by Snodgrass and Heller (1905), Fowler (1938, 1944), Rosenblatt and Walker (1963), Walker (1966), McCosker and Rosenblatt (1984), McCosker (1987), Grove and Lavenberg (1997) and McCosker (1998). Several popular treatments exist, the best of which are by Merlen (1988) and by Humann and DeLoach (2003).

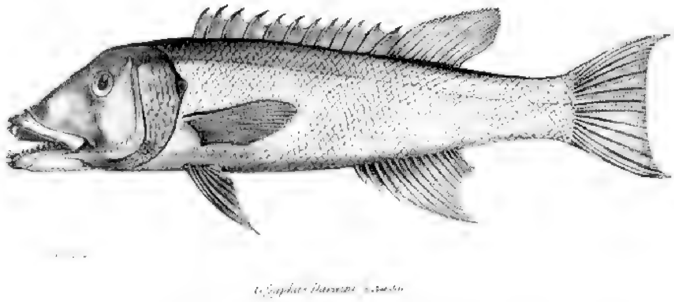

FIGURE 1. *Cossyphus darwini* (now *Semicossyphus darwini*) named by Jenyns in honor of its collector.

FIGURE 2. Galápagos sheephead (*Semicossyphus darwini*) photographed by Leighton R. Taylor. The large white shoulder blotch was not shown in Jenyns' illustration because the coloration of Darwin's specimens had faded because of their preservation in spirits.

Fishes recorded from Galápagos have grown from the 15 that Darwin collected to the 551 recorded here. Knowledge of the fauna has evolved from more than 175 years of expeditions to Galápagos which have changed dramatically with the introduction of scuba (since the 1960s) and submersibles (since the 1970s). Understanding the faunal history and relationships is far from complete and may modestly or dramatically change as new genetic techniques are applied. Our update is the result of the discoveries of many researchers and naturalists at the Galápagos and the nearby Malpelo and Cocos islands, as well as the opportunities provided us by the untethered submersibles *Johnson-Sea-Link* and *Deep-See*.

History of Ichthyological Exploration

Charles Darwin made the first collection of Galápagos fishes. The 15 specimens he collected during his nine days ashore at four different islands were later described by the Reverend Leonard Jenyns (1840-1842). Each was described as a new species. All are still valid, and six remain known

only from Galápagos. In the early nineteenth century fish taxonomy was dominated by the French, and Darwin therefore concentrated his collecting efforts in areas that had not been well-explored by French vessels. Darwin had been an avid angler early in his life and was an enthusiastic admirer of Izaak Walton's (1653) *Compleat Angler*. And, although little else is said by Darwin about Galápagos fishes in his subsequent publications, Pauley (2002, 2004:xvii) suggested that Walton's recognition of "different populations of Trout and other fish species in the British Isles, may have contributed, a decade or so later, to CD's dawning perception of within-species 'variation as a motor' of evolution."

Subsequent nineteenth century ichthyological discoveries at the Galápagos have been overshadowed by the remarkable discoveries made in the terrestrial environment. The 1891 voyage of U.S. Fish Commission steamer *Albatross* (Summers et al. 1999) was the most significant expedition of the period and resulted in the many deepwater fishes described and illustrated by Garman (1899). Slevin (1959) prepared the most comprehensive account of exploration through the mid-twentieth century. McCosker and Rosenblatt (1984), McCosker (1987), and Grove and Lavenberg (1997) have provided reviews of ichthyological research and exploration through 1995. We herein update those previous reviews to the present. The eruption of Volcan Fernandina during January 1995 provided a remarkable sample of deepslope fishes previously unknown from the archipelago (McCosker et al. 1997). Naturalist Godfrey Merlen braved aerial lava bombs and ravenous seabirds and sea lions and returned with numerous slightly damaged specimens of 22 species which were deposited at the Charles Darwin Research Station (CDRS) laboratory and at the fish collection of the California Academy of Sciences (CAS). In his honor McCosker and Long (1997) described the first Galápagos epigonid as *Epigonus merleni*; the holotype remains the only known specimen. Later in 1995, McCosker, Grant Gilmore of the Harbor Branch Oceanographic Institution (HBOI), and Bruce Robison of the Monterey Bay Aquarium Research Institute (MBARI) returned to participate in a month long exploration of deepslope fishes using the submersible *Johnson-Sea-Link* (JSL). They made dives to 1000 m at locations across the archipelago. McCosker and Smithsonian Institution (NMNH [National Museum of Natural History]) ichthyologist Carole Baldwin returned with the JSL in 1998 in order to continue the deepslope surveys and to create an IMAX film for the NMNH. The JSL submersible is well equipped to photograph (using video or still cameras) and capture specimens using anaesthetics, ichthyocides, a suction hose, a plankton funnel, or its articulated claw (Fig. 3). A rotating carousel arrangement of small enclosed aquaria provided separate compartments for specimens collected. It also allowed small fyke traps to be set and retrieved. Although slow (maximum speed 1 knot), the JSL's maneuverability and its collecting and photographic equipment proved invaluable for working along the rocky substrate of Galápagos (McCosker 1997).

The 1997/1998 El Niño (ENSO) event provided an opportunity to observe its effects in deepwater, as well as to make observations using scuba to a depth of 50 m. The observations and videos taken, as well as the collection of numerous new species and specimens previously unknown from the Galápagos, added considerably to the database, and some of that material remains unreported. It should be noted however that the JSL projects were not the first in the vicinity of Galápagos involving a submersible. Geologists aboard the submersible *Alvin* in 1977 discovered remarkable life at the hydrothermal vents along the rift zones approximately 400 km ENE of the archipelago. That was followed by numerous biological and geochemical expeditions to that area, resulting in the capture of many new creatures including a vent-endemic fish (Cohen et al. 1990).

Several brief visits by ichthyologists to Galápagos followed the CAS, HBOI, and NMNH projects. Those projects included a brief survey by McCosker and Rosenblatt in Galápagos in 1994 and an additional survey of the southern islands by McCosker, Baldwin, Gerard Wellington and John

S. Stephens in 2002. Alex Hearn of the CDRS has made several surveys in deep water using a Remote Operated Camera (ROV) in recent years. And the increasing popularity of scuba diving and tourism in recent decades has resulted in the serendipitous recording of several previously unknown and unrecorded fish and invertebrate species by underwater photographers, particularly Paul Humann.

It should also be noted that a submersible has been employed at Cocos Island (=Isla del Coco), Costa Rica, since 2005. The submersible, known as *Deep-See*, is an untethered vehicle operating to 500 m. The sub has excellent visibility and high-definition camera equipment; however, it lacks collecting devices. Many of the pictures that it has taken were shared with the authors as well as Scripps Institution of Oceanography (SIO) graduate students Brad Erisman and Brian Zgliczynski. Many of the fishes that were observed below the depth of scuba diving were unknown from Cocos and some were previously known only from Galápagos. We report herein upon some of those discoveries.

The Geological and Oceanographic Setting

Insular faunas, such as that of the Galápagos, are the result of many factors, including the remoteness and distance from the continental mainland or continental islands, the vagility of the invading species, the water depth and barriers that must be crossed, and the velocity and direction of the oceanographic currents that will carry the propagules. The oceanographic setting of the Galápagos Archipelago is key to the uniqueness of its terrestrial and marine faunas, and we herein update our previous discussion (McCosker and Rosenblatt 1984). We have relied upon similar reviews by Houvenaghel (1984), Glynn and Wellington (1983), Grove and Lavenberg (1997) and Robertson et al. (2004), as well as recent research discoveries and reports.

The Galápagos Archipelago rises abruptly from the intersection of the Cocos and Carnegie submarine ridges. The platform of the archipelago is separated from the continental mainland by a distance of 1000 km and by deep ocean no shallower than 1300 m. The platform is about 915 m below the sea surface and is surrounded by seas that average 3050 m in depth. The closest islands are Malpelo (450 km ENE) and Cocos (630 km to the NE). The archipelago is volcanic in origin and was never attached to the mainland (White et al. 1993). The Galápagos emerged at least 9 MYA (Christie et al. 1992), although habitable submarine seamounts and terraces existed prior to that date. The western islands are younger and their origin reflects the movement of the Nazsca Plate; at the time of their emergence they were about 200 km east of their current location (Cox 1983). The oceanic currents that bathe the Galápagos are key to the composition of the fish fauna. The combined effect of the northeasterly Panamic Current, the southerly South Equatorial Current and the Peruvian Coastal (or Humboldt) and Oceanic currents brings New World larvae, juveniles, and adults to the Galápagos. The westerly North Equatorial Countercurrent and the Equatorial Undercurrent are variable in strength and depth and intensified during El Niño Southern Oscillation (ENSO) events. Although the Galápagos Islands straddle the equator, the southern and eastern origin of currents, combined with local upwelling phenomena, brings cold, nutrient-rich water habitable to a temperate fauna to the southern islands. The warm Equatorial Countercurrent brings tropical species from the west and supports modest coral formations at the northern islands of Wolf and Darwin.

The aerial topography of most islands, particularly along the western coastlines, provides sheer volcanic faces which continue from the mountainsides to depths of 30-500 m, sloping beneath that to sand and boulder rubblefields. Steep and sheer profiles were selected by the JSL projects in order to maximize the habitats and depths sampled. A typical collection site is shown in Figure 4.

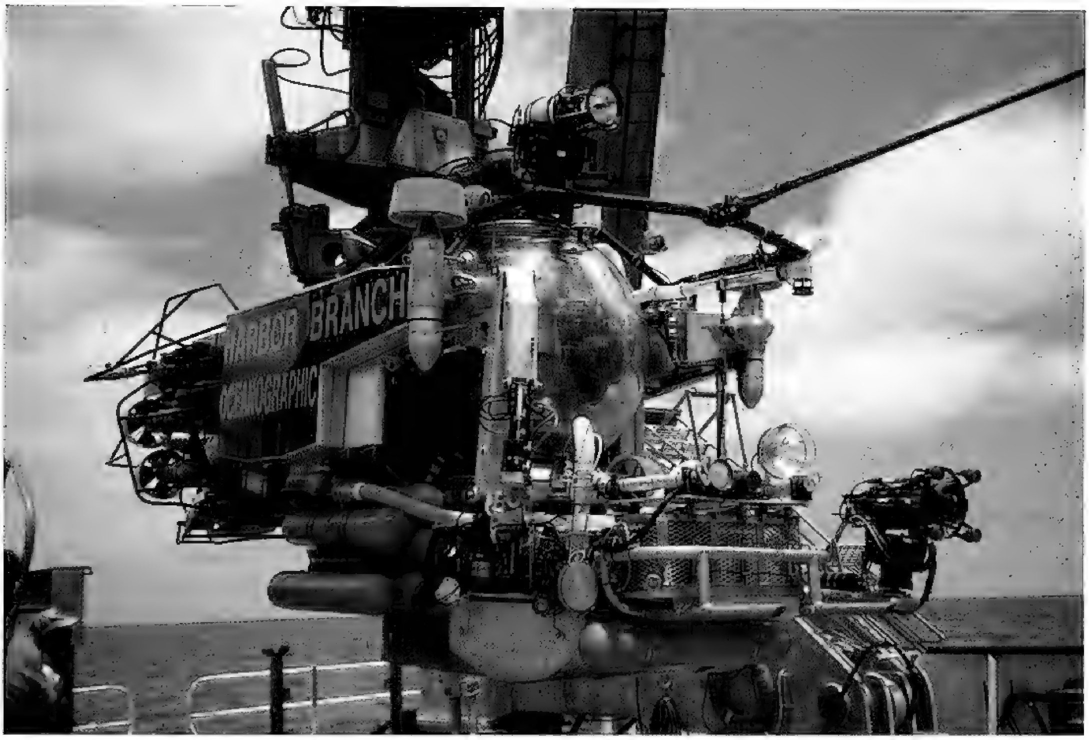

FIGURE 3. *Johnson-Sea-Link* submersible on deck of *R/V Seward Johnson*. The specimen collecting equipment, viewed in a counter clockwise direction is as follows: video camera (lower right); plankton capture funnel (upper right); articulated claw (left side); vacuum hose and rotenone dispenser (small clear tubing attached to hose) (lower left); storage basket (lower center). A laser-aimed still camera resides atop the storage basket. Not visible is the carousel of specimen-holding aquaria. Photo credit J. McCosker.

Sea temperatures in Galápagos vary widely between and within islands. Harris (1969) and Glynn and Wellington (1983) divided the archipelago into five temperature zones based on sea-surface temperature and the seabirds and corals that inhabit them. The northern islands of Darwin and Wolf are tropical and the southern islands are warm temperate. Fernandina and western Isabela approach cold temperate conditions, the southern islands of Hood and Floreana are temperate, and the central platform islands (Santa Cruz, James, Baltra, and many smaller islands) are somewhere between the extremes. The southern islands and the western shores of Isabela and Fernandina are the coldest, with the shallowest thermoclines. Sea surface monthly means vary considerably; for example, at San Cristóbal Island the means are from 18.5°C in September to 24.8°C in March, with an absolute daily minimum of 15.0°C in November (Houvenaghel 1984:48). Surface temperatures may vary between east and west sides of the

FIGURE 4. Typical volcanic reef habitat, ca. 45° slope, at 150 m off Devil's Crown, Isla Onslow. Scythe butterflyfish (*Prognathodes falcifer*) and neptheid soft corals typically inhabit this depth and habitat (JSL dive 3945).

same or nearby islands. The western shore of islands such as Fernandina and Isabela are 5-6°C cooler than the eastern shore of other nearby islands, resulting in lush algal growth and fishes more typical of the Peruvian and Chilean fauna than those from the Indo-Pacific (Rosenblatt and Hobson 1969).

New Records of Galápagos and Cocos Fishes

The opportunities provided by the *Johnson-Sea-Link* and the *Deep-See* submersibles allowed the discovery of numerous fishes and invertebrates previously unknown from the Galápagos and Cocos islands. At least 32 undescribed fish species were collected during the JSL dives and 20 have been described to date. Included are: *Anthias noeli* Anderson & Baldwin 2000; *Bellator farrago* Richards & McCosker 1998; *Coryphaenoides gypsochilus* Iwamoto & McCosker 2001; *Dibranchus discors* Bradbury, McCosker & Long 1999; *Dibranchus cracens* Bradbury, McCosker & Long 1999; *Eptatretus grouseri* McMillan 1999; *Eptatretus lakeside* Mincarone & McCosker 2004; *Eptatretus mccoskeri* McMillan 1999; *Eptatretus wisneri* McMillan 1999; *Gadella thysthlon* Long & McCosker 1998; *Halichoeres raisneri* Baldwin & McCosker 2001; *Hydrolagus alphus* Quaranta, Didier, Long & Ebert 2006; *Hydrolagus mccoskeri* Barnett, Didier, Long & Ebert 2006; *Idiastion hageyi* McCosker 2008; *Lucifuga inopinata* Cohen & McCosker 1998; *Ophichthus arneutes* McCosker & Rosenblatt 1998; *Paraliparis darwini* Stein & Chernova 2002; *Paraliparis galapagosensis* Stein & Chernova 2002; *Rajella eisenhardti* Long & McCosker 1999; *Scorpaenodes rubrivinctus* Poss, McCosker & Baldwin 2010; and *Trachyscorpia osheri* McCosker 2008. An additional 12 species remain to be described.

Many fishes and invertebrates were photographed for the first time during the JSL expeditions. Several of Garman's (1899) fishes were not illustrated and their coloration in life has not been adequately described. We herein include the first color photographs of several such species: *Myroconger nigrodentatus* (Fig. 5); *Liopropoma longilepis* (Fig. 6); *Serranus aequidens* (Fig. 7); *Serranus stilbostigma* (Fig. 8); and *Hoplostethus pacificus* (Fig. 9).

The following section is a listing of fishes previously not known from the Galápagos and/or Cocos Island. It is based on the submersible work as well as on photographs taken by underwater photographer Paul Humann. The order of presentation in this section and in Appendix 1 is alphabetically within families, following the order of families presented by Nelson (2006). Some of this information has been shared with Ross Robertson who has, with our permission, published these names without further explanation (Robertson and Allen 2002; Robertson et al. 2004). Specimens are deposited in the fish collections of the California Academy of Sciences (CAS), San Francisco; the Charles Darwin Research Station (CDRS), Puerto Ayora, Santa Cruz, Galápagos; the Instituto Nacional de Pesca (INP), Guayaquil, Ecuador; and the National Museum of Natural History (NMNH [also as USNM]), Washington, D.C.

The new records of Galápagos and Cocos island fishes includes: ***Chimaera* sp.**: two specimens of this undescribed species were collected in deep water (915 m) off Plaza Island (CAS 201855) and off Santa Cruz Island (CAS 222061, at 905 m); ***Hydrolagus* sp.**: a third species of chimaera observed and collected using the JSL remains to be described. Specimens include CAS 201872 from 623 m off Isla Fernandina and CAS 201873 from 905 m off Isla Santa Cruz. This species also occurs off Cocos Island (Douglas Long, pers. com.). ***Apristurus* sp.**: this undescribed epibenthic catshark was photographed and captured (CAS 201852) at 915 m off Isla Santa Cruz by the JSL during July, 1998, and will be described by Kazuhiro Nakaya. ***Bythaelurus* sp.**: this undescribed Galápagos catshark was observed and captured at 428-562 m at Darwin and Marchena islands, and will soon be described (McCosker, Compagno & Baldwin, in prep.). ***Galeus* sp.**: collected at San Cristobal, Fernandina, Darwin, and Genovesa islands between 460-580 m; those specimens repre-

FIGURE 5. *Myroconger nigrodentatus* photographed from JSL submersible at 220 m along a 70° slope off Devil's Crown, Isla Onslow (JSL dive 3945).

FIGURE 6. *Liopropoma longilepis* photographed from JSL submersible at 209 m along a 60° slope off Devil's Crown, Isla Onslow (JSL dive 3945).

FIGURE 7. *Serranus aequidens* photographed from JSL submersible at 200 m along a sand and volcanic rubble bottom, on top of seamount off Isla San Cristobal (JSL dive 3935).

FIGURE 8. *Serranus stilbostigma* photographed from JSL submersible at 200 m along a sand and volcanic rubble bottom, on top of seamount off Isla San Cristobal (JSL dive 3935).

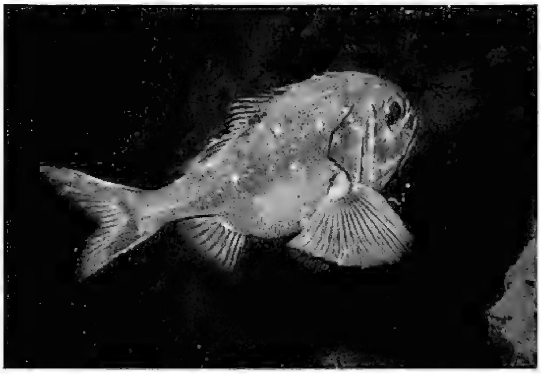

FIGURE 9. *Hoplostethus pacificus* photographed from JSL submersible at 600 m off Cabo Hammond, Isla Fernandina (JSL dive 3952).

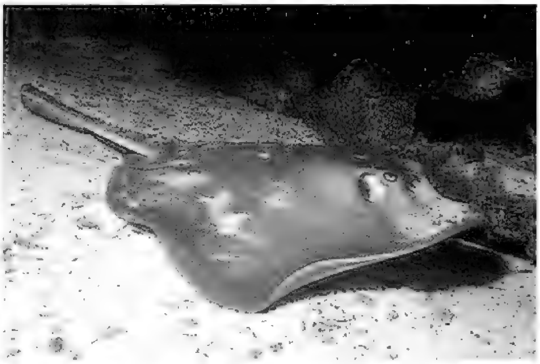

FIGURE 10. *Dasyatis* sp. off north shore of Devil's Crown, Floreana Island, at 15 m. Photo credit Paul Humann©.

sent an undescribed species (Douglas Long, pers. comm.). ***Echinorhinus cookei***: the Prickly shark was observed and photographed at the Galápagos and Cocos islands; a report by Douglas Long is in preparation. ***Dasyatis* sp.**: a species of *Dasyatis* was photographed by Paul Humann and identified in his guide (Humann and DeLoach 2003:216-217) as *Dasyatis brevis*. Humann subsequently photographed (Figs. 10-11) this ray at several locations (off Seymour, Baltra, Plazas, and Floreana islands) at depths of 15-20 m. We are advised by J. McEachern in litt. 14 Jan. 2010) that this may be an undescribed species of *Dasyatis*. ***Torpedo peruana***: described by Chirichigno (1983) as *Torpedo tremens peruana*, this species was photographed and collected by the JSL at Isabela (CAS 86818) and Fernandina islands at 513 m and at 200 m, respectively, and off Española Island (USNM 352257) at 365 m. Paul Humann photographed individuals at 20-30 m off Punta Vicente Roca and Tagus Cove, Isla Isabela. Another underwater photographer, Kendra Choquette-d'Avella, photographed specimens in midwater (Fig. 12) off Cabo Marshall and Punta Vicente Roca, Isla Isabela in 2004, at depths of 20-50 m. ***Myroconger nigrodentatus***: this colorful striped eel (Fig. 5), originally described by Castle and Bearez (1995) from a fish market specimen in Manabí, Ecuador, was occasionally found on deep Galápagos and Cocos Island reefs at 220-345 m. Several Galápagos specimens were collected from a seamount SE of Isla San Cristobal (CAS 86745, CAS 86746, CAS 86753), from Isla Fernandina (CAS 86517), and from Isla Floreana (CAS 86426), and seen but not collected at Baltra, Española, and Isabela islands. ***Echidna nebulosa***: the Snowflake moray is widespread in the Indo-Pacific and has been found at several tropical eastern Pacific localities including Clipperton and Cocos islands (Allen & Robertson 1994); however, it has not previously been reported from the Galápagos. Specimens in the Academy collection (CAS 50079, 4, 63-205 mm, and SU 37378, 170 mm) were collected in tidepools at Tower Island. They have also been photographed by Dee Wescott at Cabo Marshall in August, 2004, and by Paul Humann and Pierre Constant in September 2006. ***Gymnothorax angusticeps***: this moray has been infrequently reported since its description from off Talara, Peru, by Hildebrand and Barton (1949). A large moray captured by the JSL using hook-and-line at 227 m off Seymour Island (CAS 86810, 975 mm SL) proved to be of this species. It has 4/74/170 vertebrae. The species has also been photographed at 42 m at the NE corner of Malpelo Island by Clay Bryce (Robertson and Allen 2002, image labeled as *Gymnothorax castaneus*) and was commonly seen from the *Deep-See* submersible at Cocos Island along steep rock reefs (150-200 m depth). ***Bathycongrus* sp.**: this new deepwater (563-985 m) congrid, collected over sand bottoms (CAS 86740, 2, 185-187 mm TL, and CAS 86751, 184 mm TL) off Fernandina and San Salvador islands, will be described by D. Smith and J. McCosker. **"*Ophisoma*" sp.**: another undescribed deepwater (570-593 m) congrid was collected from sand bottoms off Peru and Galápagos (CAS 201870, Cabo Douglas, Isla Fernandina), and, like its congener *O. prorigerum*, will be placed in another yet-to-be determined genus (D.G. Smith, in litt.). ***Argentina aliceae***: a specimen (CAS 86571, 137 mm SL) of *Argentina aliceae*, known from central America to Peru, is the first argentinid known from Galápagos. It was collected by the JSL off Cabo Douglas, Fernandina Island, at 412 m above a sand and rubble bottom. ***Physiculus nematopus***: widely distributed from California to Panama, the first Galápagos specimens were collected at approximately 300 m off Santa Maria, Española, and Fernandina islands. ***Monomitopus malispinosus***: collected by the JSL off Roca Redonda at 550 m, this specimen (CAS 86735) appears to be the first known Galápagos specimen. ***Phenacoscorpius* sp.**: several specimens that may be conspecific with a species from the Nazsca and Sala y Gomez ridges were collected in 460-515 m at several Galápagos locations, and will be reviewed by Hiroyuki Motomura (in prep.). ***Pontinus* spp.** and ***Pontinus vaughani***: three undescribed species as well as *P. vaughani*, previously unreported from Galápagos, were photographed and captured at various locations. They will be treated by Poss et al. (in prep.). ***Scorpaena cocosensis***: previously known only from the holotype collect-

ed at Cocos Island, the first Galápagos specimen (CAS 86522) was captured at Darwin Island at 93 m (Motomura and McCosker 2009). ***Scorpaenodes rubrivinctus***: an undescribed species was collected and observed at several Galápagos and Cocos Island locations at 203-412 m and was recently described by Poss, McCosker and Baldwin (2010). ***Bellator farrago***: was described by Richards and McCosker (1998) from specimens collected at Santa Cruz, Tower, and Isabela islands to a depth of 462 m. Many more specimens were observed and collected at additional Galápagos locations during the 1998 expedition. This species has now been observed by McCosker at Cocos Island. ***Liopropoma longilepis***: this serranid (Fig. 6), known only from the holotype from the Gulf of Panama, was observed and collected at Galápagos by the JSL at depths of 110-290 m at Floreana (CAS 86404, 2, 143-181 mm SL), Española (CAS 86417, 149 mm SL), and observed but not collected at Baltra Islands and at a seamount SE of San Cristobal. Like *L. fasciatum* it occupies rock reefs and prefers crevices within near-vertical faces. It was also observed (by JM) at 164 m at the north side of Cocos Island from the submersible *Deep-See*.

FIGURE 11. Aggregation of *Dasyatis* sp. at 20 m along an island wall in the channel between Baltra and Seymour islands. Photo credit Paul Humann©.

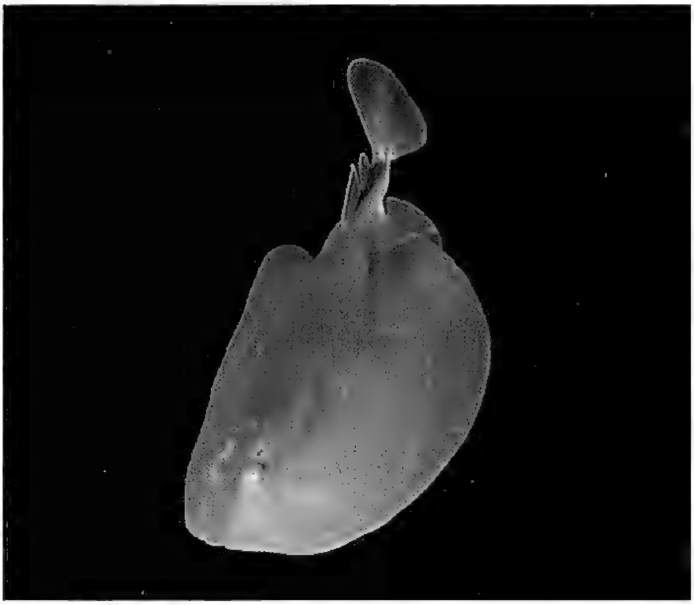

FIGURE 12. *Torpedo peruana* photographed off Cabo Marshall, Isla Isabela, at 20-50 m. Photo credit Kendra Choquette-d'Avella©.

Serranus aequidens: two specimens (CAS 213430, 85-116 mm SL) were collected over a coarse sand and boulder bottom at 486 m atop a seamount SE of Isla San Cristobal. They were identified using the original description and compared to specimens from the Gulf of California (SIO 65-248) with which they are conspecific. Other specimens were photographed (Fig. 7) from the submersible in similar habitats at depths as shallow as 195 m. ***Serranus stilbostigma***: subsequent specimens of this species have not been recorded since Jordan and Bollman's (1890) description of the holotype collected by the *Albatross* off Galápagos in 45 fms (82 m). We observed and filmed several individuals at depths of 195-203 m above a coarse sand and boulder bottom atop a seamount (the same

locations where *S. aequidens* were seen and collected). The specimen that we collected (CAS 86415, 146 mm SL) (Fig. 13) and those that we observed were dramatically patterned with a large black blotch at the base of the soft dorsal extending onto the fin. A large creamy blotch extends along the flank at a 110° angle from just below the black blotch to the appressed tip of the pelvic fin. Extending along the lateral line to the base of the tail are a dozen smaller black spots. Jordan and Bollman's original description (p. 159) stated "color reddish brown (probably crimson in life), becoming paler beneath, breast somewhat orange." We did not observe any of the red or orange coloration that they mentioned. ***Lutjanus guttatus***: the Spotted rose snapper, widely distributed from the Gulf of California to Peru, is reported for the first time from the Galápagos. Several individuals were captured by hook-and-line fishing off Puerto Villamil in June 1998. Fish were caught while the ship was at anchor over a 10-15 m sand and boulder bottom. Specimens include CAS 201811 (415 mm SL), USNM 352023 (420 mm SL), USNM 352050 (360 mm SL) and specimens given to the Parque Nacional Galápagos. ***Pristipomoides zonatus***: the first known Galápagos individual of the Indo-Pacific Oblique-banded snapper was listed by Robertson et al. (2004: Table 1) on the basis of a fish taken by hook-and-line fishing at Punta Albemarle, Isabela, on 10 September 1994 and photographed by Godfrey Merlen. The fish had been gutted (Fig. 14) and was subsequently eaten. In that there are no other known eastern Pacific sightings of this species we presume that this individual was a vagrant. ***Chaetodon unimaculatus***: a Teardrop butterflyfish, photographed by Paul Humann at 10 m off Wolf Island in 2002, represents the first Galápagos record and is an additional Indo-Pacific vagrant. ***Halichoeres adustus***: the Black wrasse was photographed by Paul Humann at 15 m off the east side of Wolf Island in 2000 and 2002. ***Halichoeres melanotis***: the Golden wrasse was photographed by Humann at Devil's Crown, Onslow Island, in 2002. ***Halichoeres raisneri***: this wrasse is now known from Cocos and Malpelo islands. As Baldwin and McCosker's (2001:97) description was in press, they were told of a male specimen from Cocos Island that was probably this species. JM subsequently observed several individuals at depths of 150-190 m while sub diving at Cocos in 2007. Sandra Bessudo of the Fundación Malpelo forwarded photographs taken by a ROV along a coarse sand bottom at 100 m off Malpelo Island. The pictures clearly include individuals of *H. raisneri* that are identical in coloration to that of the live Galápagos paratype (Baldwin & McCosker 2001:Fig. 4 bottom). ***Xyrichtys* sp.**: Benjamin Victor (in litt., 23 March 2009) advises us that he has collected juveniles of an undescribed Galápagos species for which no adult is known. ***Entomacrodus chiostictus***: we discovered the eastern Pacific shallow water Rock blenny along rocky cliff faces of Darwin and Fernandina islands. Numerous individuals were seen and specimens were collected within the wave splash zone by McCosker and Carole Baldwin in June 1998 (CAS 201889, 2, 19-44 mm SL; CAS 203929, 27.5 mm SL; CAS 205832, 4, 39.5-48 mm SL; USNM 365991, 4, 40.3-46.4 mm SL; USNM 366733, 24.7 mm SL). It has apparently been overlooked by most divers and ichthyologists because of its habitat. ***Sphyraena barracuda***: the Great barracuda, a circumtropical resident except for the eastern Pacific (a specimen is also known from Pacific Panama), was caught (Fig. 15) by hook-and-line fishing by Tui De Roy and Mark Jones of the Galápagos in July 1994 in Puerto Ayora, Isla Santa Cruz. Another was seen by Paul Humann off Wolf Island in April 1994. We consider those individuals to be vagrants. ***Benthodesmus tenuis***: a Slender frostfish was collected off Cabo Hammond, Fernandina Island, at 580 m (CAS 86742, 452 mm SL). ***Hippoglossina bollmani*?**: a *Hippoglossina* (CAS 86410, 151 mm SL) was collected from Santa Maria Island (off Isla Española) at 304 m. It was examined by the late D.A. Hensley who found it to be either an undescribed species of *Hippoglossina* or an abnormal *H. bollmani*, a species known from Galápagos. We mention it here but do not yet consider it to be a separate species and do not include it in our faunal calculations. ***Monolene maculipinna***: the first Galápagos individual (CAS 86411, 121 mm SL) was captured at

330 m on a steep sand slope at Santa Maria Island, during the same dive as that which captured the *Hippoglossina*. ***Arothron nigropunctatus***?: an individual which appears to be the Blackspotted puffer was observed and photographed (Fig. 16) but absent the specimen we cannot identify it with certainty. This adult puffer, approximately 20 cm total length, was discovered by snorklers on 4 June 2005 at Tower Island and observed by JM. It was seen by a diver along the wall of the bay at "Prince Phillip's Steps" at approximately 8 m depth, who captured it by hand and returned with it to the surface and was then released. (It had swallowed water, as is its normal defensive behavior.) Its brown body coloration with small dark body spots was typical of the species, however the white snout mask was very pale. Its coloration was unlike that of the sympatric *A. meleagris* or *A. hispidus*. We are unaware of other photographs or reports of *A. nigropunctatus* from the eastern Pacific.

FIGURE 13. *Serranus stilbostigma* (CAS 86415, 146 mm SL), photographed soon after capture above sand bottom, depth 203 m, on top of seamount off Isla San Cristobal. Photo credit J. McCosker.

FIGURE 14. *Pristipomoides zonatus* caught by hook-and-line at Punta Albermarle, Isla Isabela. Photo credit Godfrey Merlen©.

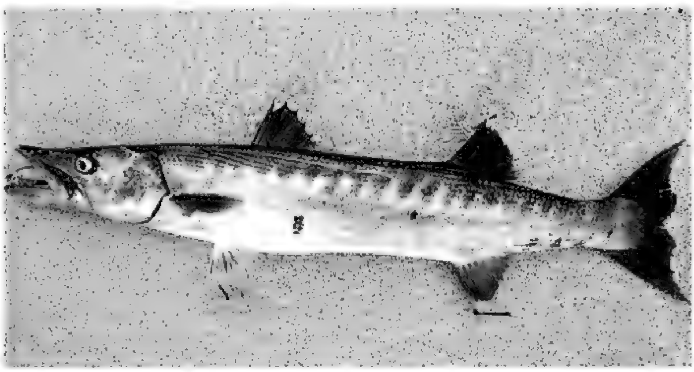

FIGURE 15. *Sphyraena barracuda* captured by hook-and-line off Puerto Ayora, Isla Santa Cruz. Photo credit Tui de Roy©.

We report upon what appears to be the first introduced and established freshwater fish to Galápagos. The Mozambique tilapia *Oreochromis mossambicus*, native to South Africa but now widely distributed elsewhere by humans, was discovered on 14 February 2006 in El Junco Lagoon, San Cristobal Island (Godfrey Merlen and Veronica Toral-Granda, in litt., 17 Feb. 2006). This invasive species is now apparently reproducing and established in the lagoon, and has been introduced into other small freshwater farmponds.

McCosker (1998) corrected several records of species incorrectly reported from Galápagos. To that, we add Appendix 1 and explain that previous records of *Chaunax latipunctatus*, *Hypoplectrodes semicinctus* and *Lactoria diaphana* from Galápagos are also invalid.

Faunal Composition

The origin and ancestry of the Galápagos fish fauna have been reviewed by previous authors (Heller and Snodgrass 1903; Rosenblatt and Walker 1963; Walker 1966; McCosker and Rosenblatt 1984; Grove and Lavenberg 1997; and McCosker 1998). Those previous analyses have not changed dramatically with the inclusion of new species and the new records that we have added. As well, the ENSO events during the last quarter century have resulted in numerous sightings, photographs, and collections of Indo-Pacific vagrant species, particularly at the northern islands of Darwin and Wolf. The deepwater additions are certainly biased in that similar work has not been accomplished at other eastern Pacific locales and the deepslope studies at Galápagos and Cocos are far from complete. We will upgrade previous listings and compare the Galápagos ichthyofauna to that of similar remote islands.

The resident fishes of Galápagos to a depth of 60 m are now fairly well known. The fauna is larger than those of other eastern Pacific islands, despite their distance from the mainland, in that the area of Galápagos is larger and the variety of habitats is greater. On the basis of published and unpublished records as well as our own collections we now record 550 species representing 128 families (excluding mesopelagic species). (We exclude the introduced cichlid *Oreochromis mossambicus* from discussions in this section.) For comparative purposes (particularly with studies by J.E. Randall), we remove such pelagic Galápagos fishes as the exocoetids and echeneids, and those living deeper than 200 m, and thereby recognize 463 species. This is comparable to Randall's (2007) listing of 612 species within the Hawaiian archipelago. It may also be compared to the ichthyofaunas of Easter Island (139 species, cf. Randall and Cea, in prep.), Rapa (256 species, cf. Randall 1998) and Cocos Island, Costa Rica (270 species, cf. Robertson and Allen 2002; Garrison 2005).

The Galápagos ichthyofauna is a distinctive subunit of the Panamic province. (See Appendix 1 for the listing and relationships of the fishes of Galápagos.) Nearly half of its species (247 species, 44.8%) are shared with the Panamic fauna to the east, many of which range from southern Mexico to northern Ecuador. The remainder of shared eastern Pacific species are also in Peru and/or Chile (32 species, 5.8%), and are typified by the large wrasses and certain groupers.

Seven Galápagos species (excluding those pantropical species) are shared with the eastern Pacific and the western Atlantic (*Sphyrna tiburo*, *Mugil curema*, *Agonostomus monticola*, *Epinephelus mystacinus*, *E. niphobles*, *Eucinostomus argenteus*, and *Gerres cinereus*). An eighth, *Guentherus altivelis*, is known from the eastern Pacific and the eastern Atlantic. New World transisthmian species such as these are currently under review using genetic techniques (Lessios et al. 1995; Bermingham et al. 1997). These studies have demonstrated that although the western Atlantic and eastern Pacific forms of such fishes as *Abudefduf saxatilis* and *A. troschelii* and *Paranthias furcifer* and *P. colonus* are closely related congeners and were previously considered to be transisthmian, enough differentiation exists that they should be recognized as sibling species. A curious distribution involves the shallow water Galápagos sparid *Archosargus pourtalesii*, whose closest relative is from the Atlantic but no additional eastern Pacific congener is known.

Eighty-four species (15.2%) are found worldwide in the tropics and we have listed them as cosmopolitan. These include the large sharks, rays, pufferfishes, dolphinfishes, tunas, many exocoetids and the echeneids.

Numerous Indo-Pacific shorefishes, which total 88 species (15.9% of the fauna), are found along the warmer shores of several islands and are particularly abundant at the northern islands of Wolf and Darwin. The majority of those species are also found in the Line Islands and/or the Marquesas and were carried to the Galápagos by the Equatorial Counter-current (Robertson et al.

FIGURE 16. Adult *Arothron nigropunctatus*? observed and released at Tower Island. Its identity is uncertain. Photo credit Al Grigarick©

2004). Several species that we have listed as IP in Appendix 1 (*Encheliophis dubius*, *Caranx caballus*, *Euthynnus lineatus*, and *Balistes polylepis*) are common only to Hawaii and the eastern Pacific (Randall 2007). The kyphosid *Sectator ocyurus* is presumed to be eastern Pacific in origin (Rosenblatt et al. 1972) and inhabits Hawaii, French Polynesia, and the Izu and Mariana islands (Randall 2007). Randall (2007) has proposed that many of those species that migrated from east to west did so as juveniles associated with drifting algae or flotsam.

Many Galápagos species are recorded as vagrants (primarily chaetodontids, muraenids and tetraodontids) because of their irregular arrival and apparent lack of reproductive populations. It is thought that ENSO events enhance the migration of Indo-Pacific fish larvae across the central Pacific due to the doubling of the velocity and the tripling of the latitudinal spread of the North Equatorial Counter-current at that time (Grigg and Hey 1992; Robertson et al. 2004). However, this is countered by negative factors associated with higher temperatures such as decreased productivity, shorter pelagic larval duration, and possibly smaller size at metamorphosis (Robertson et al. 2004). In any case, there are few records of the appearance of Indo-Pacific fishes precisely associated with ENSO events.

By removing the 14 presumed vagrants from the resident Galápagos fish fauna, the total becomes 536 species. This reduces the proportion of Indo-Pacific elements to 13.8% and modestly increases the proportion of the other components (eastern Pacific becomes 48.8%, Peru/Chile 6.3%, Cosmopolitan 16.6%, Galápagos endemics 14.8%, and shared Galápagos, Cocos and/or Malpelo endemics 19.4%).

We have not included the benthopelagic fish fauna of the Galápagos in this analysis. Cohen and Haedrich (1983) summarized the fishes associated with the Galápagos thermal vent region and found approximately 20 species. (Several subsequent descriptions have occurred.) They suggested that 50-75 benthopelagic fish species occur at depths close to 2,500 m in the tropical eastern Pacific and we presume that many exist at those depths in the vicinity of the Galápagos Archipelago but have yet to be discovered there. At this time we have no way to estimate the possible degree of endemism amongst the Galápagos benthopelagic fishes.

The endemic species provide biologists with an opportunity to speculate about the history of the Galápagos ichthyofauna. That paradigm is particularly useful to zoogeographers and island biogeographers in that the Galápagos lie within the path of a variety of currents (Panamic, Equatorial Counter-current, and Humboldt) that are the source of the fauna and create the extraordinary assemblage of cool and warm water denizens. The geological history of Galápagos indicates that there is no evidence for vicariant events. Also, the nearest oceanic islands, Malpelo and Cocos, share many of the Galápagos fishes, and could act as stepping stones from the Panamic region. The endemism of Galápagos fishes is particularly striking, and not unlike that of the Hawaiian Islands

or other oceanic outposts (McCosker and Rosenblatt 1984). The degree of endemism varies between families of fishes and relates to the familial similarities within and the biological differences between families. For example, the families showing a high degree of endemism are the Dactyloscopidae (three of four), the Labrisomidae (six of eight, although two are shared with Cocos or Malpelo), the Chaenopsidae (three of three), the Pomadasyidae (four of nine), and the Sciaenidae (three of five). The New World labrisomids are excellent candidates for endemism in that the eight species are small reef-associated blennioids with a short larval life and sedentary adults that attach their eggs to solid surfaces. The non-endemic labrisomid *Labrisomus multiporosus* has the widest geographic distribution among its Pacific congeners and is reported to have an unusually long larval life (Hubbs 1953; Rosenblatt and Walker 1963).

Historically, the degree of endemism was presumed to be clearly related to the vagility of the larval and/or adult stages and the duration of larval life. Those forms which are strong pelagic swimmers, such as the carangids and thunnids, can easily cross the 1000 km barrier between the archipelago and the mainland. Those with protracted larval stages which are well-suited to pelagic life, such as some serranids, some blennies, and eels, or those which associate with floating detritus, are also able to cross such deep water gaps. The above discussion, which is a summary of McCosker and Rosenblatt's (1984) analysis, has been questioned by Victor and Wellington (2000) after their analysis of the Pelagic Larval Duration (PLD) of 29 labrid species and 20 pomacentrids. They found no significant relationship between the PLD and the distance traversed between islands and archipelagos. Extreme examples such as the labrids *Novaculichthys taeniourus*, which has a mean PLD of 50.3 days and ranges over 25,269 km, and *Xyrichtys* sp. (a Galápagos endemic), which has a mean PLD of 70.7 days and a range of 100 km, counter the assumption that a long PLD decreases the likelihood of endemism. They concluded that PLD, swimming ability, larval behavior and ecology, the ability to delay larval metamorphosis, and other independent factors including local abundance, as well as possible ecological constraints such as competition or specific habitat requirements, provide "little evidence for any unifying hypothesis (to explain shorefish distribution) and the more data are gathered, the less clear the picture becomes." (Victor and Wellington 2000:246.)

With the addition of several new deepwater species, we now recognize 75 nearshore and deep-slope fishes to be unique to Galápagos. (As stated above, it is likely that many or most of the endemic species living below 200 m may turn out to be more widely distributed.) There are as well 23 species that are shared with Malpelo and/or Cocos Island. Considering the entire Galápagos fauna to be 550 species (not including mesopelagics), Galápagos endemism is 13.6%. If the mesopelagics, vagrants, scombrids, echeneids, and exocoetids are removed, the total fauna is 505 species, of which 14.8% would be endemics. Twenty additional species (all found above 200 m) are known only from Galápagos, Cocos and/or Malpelo, and their combined endemism is thereby 17.8%, or 19.4% if the mesopelagics, vagrants, scombrids, echenedis, and exocoetids are removed from the calculation.

The distributions of eastern Pacific shallow water shorefishes are fairly well known. Interesting comparisons can be made between widespread eastern Pacific species and those that are endemic to Galápagos, Cocos, and/or Malpelo. Eels of the families Ophichthidae and Muraenidae provide an instructive comparison. All true eels have leptocephalus larvae and are presumed to be quite vagile. Twenty-one muraenids are known from Galápagos; several of the 11 Indo-Pacific species are probably non-resident vagrants, the remainder are elsewhere in the eastern Pacific, and none are limited to Galápagos, Cocos, or Malpelo. There are 11 Galápagos ophichthids, of which two are endemics (*Callechelys galapagensis* and *Ophichthus arneutes*), two are shared with Cocos Island (*Ophichthus rugifer* and *Quassiremus evionthas*) and one is endemic to Galápagos, Cocos,

and the Revillagigedo Islands (*Paraletharchus opercularis*); none are present in the Indo-Pacific. The distribution of congrid eels is much like that of the ophichthids. Among the blennioids the degrees of endemism is quite variable. For example: none of the four blenniids are endemic; all three of the Galápagos chaenopsids are endemic, and each island has one endemic species of *Acanthemblemaria* (*A. castroi* from Galápagos, *A. atrata* from Cocos, and *A. stephensi* from Malpelo); and each island has but one tripterygiid and it is endemic (*Lepidonectes corallicola* from Galápagos, *Axoclinus cocosensis* from Cocos, and *A. rubinoffi* from Malpelo). Gobiids display a mixed degree of endemism: Galápagos and Cocos share *Elecatinus nesiotes*; Galápagos, Cocos and the Revillagigedo Islands share *Lythrypnus rhizophora*; *Bathygobius l. lineatus*, *Chriolepis tagus*, and *Lythrypnus gilberti* are Galápagos endemics; and *Coryphopterus urospilus* and *Lythrypnus dalli* are widely distributed in the eastern Pacific. The shallow water ogcocephalid species of *Ogcocephalus* are curious in that *O. darwini* is not uncommon at Galápagos, and is known from a specimen from Malpelo and one from Peru. Cocos Island has a quite different species, *O. porrectus*.

The status of the pomacentrid *Azurina eupalama*, described from Hood and Charles islands in 1893, is an enigma. Its behavior is such that it was not easily overlooked by snorklers or scuba divers and it was not uncommonly encountered in numerous Galápagos open water localities above rocky bottoms in 5-30 m. It has not been observed at Galápagos since 1977. It was purportedly collected once at Cocos Island in 1925 by "C.W. Beebe et al." during the *Arcturus* expedition. The 63 specimens (AMNH 8675) were presumably collected using dynamite. It has not subsequently been sighted at Cocos Island by the first author during two scuba expeditions to Cocos Island (2000 and 2007) and several scuba expeditions by W.A. Bussing of the University of Costa Rica. Bussing (in litt. 2009) stated that "On the 1972 *R/V Searcher* Expedition we rotenoned lots of reefs around the island and never got *Azurina*. We poisoned on other pre-1982/1983 [trips] and no *Azurina*. Although I had never seen the fish, I was aware of such a species, so I imagine I would have recognized it while just diving along the reef if it had been present." In that the *Arcturus* expedition visited and collected at Galápagos prior to and after visiting Cocos (Beebe 1926), we suspect that the locality of the AMNH specimens is erroneous, and therefore recognize *Azurina eupalama* to be a Galápagos endemic. It has been proposed by Grove and Lavenberg (1997:473-474) that it might have become extinct as a result of the 1982/1983 ENSO event.

The analysis of Galápagos deepwater fish endemism is preliminary at this point; however, it is interesting to consider that all Galápagos myxinids (4 of 4) are endemic, three of four chimaerids are endemic and the fourth is shared with Cocos Island, four of 15 macrourids are endemic, three are shared with Peru or Chile, and the remainder are shared with the Panamic province (Iwamoto and McCosker 2001), six of eight bythitids are endemic, the remainder shared with the Panamic province, and three of six ogcocephalids are endemic, one (*Dibranchus erinaceus*) is shared with Cocos, one (*Ogcocephalus darwini*) is shared with Malpelo and has been found once off Peru (Bradbury et al. 1999).

Numerous authors have recently examined the genetic relationships of western Atlantic, eastern Pacific, and Indo-Pacific fish populations using mtDNA and allozymes. Galápagos material was unavailable for most of those studies. Lessios et al. (1995) did have access to *Abudefduf troschelii* from Galápagos, Panama, and Cabo San Lucas, Mexico. Gene frequencies using mtDNA COI agreed with morphological measurements and meristics, and populations of *A. trochelii* were very similar or identical at all localities. They did however find that Galápagos and Cabo San Lucas individuals were more similar to each other than to those from Panama, a finding that supports previous studies of the insular nature of the Cabo San Lucas locality. Lessios and Robertson (2006) subsequently compared the mtDNA of 20 species of nearshore reef fish (primarily acanthurids, scarids and labrids, and a variety of other species) common to the eastern Pacific and the central

Pacific, the majority of which exist at Galápagos (their study however did not include Galápagos specimens). Only two of the 20 species (*Doryrhamphus excisus* and *Cirrhitichthys oxycephalus*) had haplotypes that were significantly different, thereby supporting current taxonomic assumptions about those species (based on morphometrics and meristics) and indicating that considerable genetic exchange is ongoing. This supports the early conclusion of Rosenblatt & Waples (1986) based on alloyzyme analysis. Research underway by Giaccomo Bernardi of the University of California at Santa Cruz and his colleagues will compare the mtDNA of Galápagos shorefishes with those from Cocos Island and other eastern Pacific locations and should provide the most comprehensive comparisons to date.

The archipelago has no naturally occurring primary freshwater fishes. As reported above, the introduction of the Mozambique tilapia *Oreochromis mossambicus* in 2006 or earlier to El Junco Lagoon, San Cristobal Island, has resulted in an established population of that invasive species. The only other purported freshwater fish found in a Galápagos lake is a gerreid identified as "a species of *Xystaema*" by Colinvaux (1968:592-593) from Beagle Crater, Isabela. Beagle Crater is a highly saline lake that is connected tidally to the sea.

Remaining Galápagos Ichthyological Studies

As we have said, Galápagos shorefishes to a depth of 60 m are fairly well known. At least one new chaenopsid (*Ekemblemaria* sp., observed in 5 m at Plazas Island by McCosker et al. (1978) remains uncollected and undescribed. Other species are known only from the holotype (e.g. *Chriolepis tagus*, collected in 1934 in 10-18 fms in Tagus Cove). The tidepool labrisomid *Cottoclinus canops* has only been found once, in a tidepool at Pta. Suarez, Española (Hood), despite efforts to rediscover it at the same and nearby localities (McCosker et al. 2003). Although some dredging and bottom-trawling above the archipelago's central platform were undertaken by the Allan Hancock expeditions during the 1940s, it was certainly not extensive enough to adequately sample the habitat(s). During the few JSL dives that were made at such locales several new species of fishes were discovered, indicating that additional benthic collecting will most probably result in other additions. And most importantly, deepslope and benthic collections below 500 m will make numerous remarkable discoveries, as noteworthy as were those of the *Albatross* expeditions and that of Charles Darwin aboard the *Beagle*.

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Appendix 1

Fishes of the Galápagos Archipelago*

*Includes benthopelagic and epipelagic species within 50 km of shoreline, but excludes mesopelagics. Abbreviations are: (EP=Eastern Pacific; EP/A= Eastern Pacific and Atlantic; IP=Indo-Pacific; IP(V)= Indo-Pacific vagrant; G=Galápagos endemic; C=Cocos; M=Malpelo; R=Revillagigedos; PC=Peru and/or Chile; W=circumtropical). IP species limited to Hawaii are listed as IP and are discussed in the text. Date, spelling, and authorship of publication are based on Eschmeyer and Fricke (2009).

BRANCHIOSTOMATIDAE
PC *Branchiostoma elongatum* (Sundevall 1853)

MYXINIDAE
G *Eptatretus grouseri* McMillan 1999
G *Eptatretus lakeside* Mincarone & McCosker 2004
G *Eptatretus mccoskeri* McMillan 1999
G *Eptatretus wisneri* McMillan 1999

CHIMAERIDAE
G *Chimaera* sp.
G *Hydrolagus alphus* Quaranta, Didier, Long & Ebert 2006
G *Hydrolagus mccoskeri* Barnett, Didier, Long & Ebert 2006
GC *Hydrolagus* sp.

HETERODONTIDAE
PC *Heterodontus quoyi* (Fréminville 1840)

RHINCODONTIDAE
W *Rhincodon typus* Smith 1828

ALOPIIDAE
W *Alopias pelagicus* Nakamura 1935
W *Alopias superciliosus* (Lowe 1839)

LAMNIDAE[1]
W *Isurus oxyrinchus* Rafinesque 1810

SCYLIORHINDIDAE
EP *Apristurus kampae* Taylor 1972
G *Apristurus* sp.
G *Galeus* sp.
G *Bythaelurus* sp.

TRIAKIDAE
C/A *Mustelus mento* Cope 1877
EP *Mustelus* sp.[2]
PC *Triakis maculata* Kner & Steindachner 1866

CARCHARHINIDAE
IP *Carcharhinus albimarginatus* (Rüppell 1837)
EP *Carcharhinus altimus* (Springer 1950)
W *Carcharhinus falciformis* (Müller & Henle 1839)
W *Carcharhinus galapagensis* (Snodgrass & Heller 1905)
EP *Carcharhinus limbatus* (Müller & Henle 1839)
W *Carcharhinus longimanus* (Poey 1861)
W *Carcharhinus plumbeus* (Nardo 1827)
W *Galeocerdo cuvier* (Peron & Lesueur 1822)
EP *Nasolamia velox* (Gilbert 1898)
W *Prionace glauca* (Linnaeus 1758)
IP *Triaenodon obesus* (Rüppell 1837)

SPHYRNIDAE
W *Sphyrna lewini* (Griffith & Smith 1834)
W *Sphyrna mokarran* (Rüppell 1837)[3]
EP/A *Sphyrna tiburo* (Linnaeus 1758)
W *Sphyrna zygaena* (Linnaeus 1758)

ECHINORHINDAE
IP *Echinorhinus cookei* Pietschmann 1928

SQUALIDAE
IP *Centroscyllium nigrum* Garman 1899
W *Isistius brasiliensis* (Quoy & Gaimard 1824)

TORPEDINIDAE
PC *Torpedo peruana* Chirichigno 1983

[1]The white shark, *Carcharodon carcharias*, was reported from Galápagos by Grove and Lavenberg (1997:57) on the basis of an observation by a Galápagos guide, however until a photograph or specimen is recorded we are hesitant to include this species.

[2]An undescribed species from Mexico, Ecuador and Galápagos (P. Heemstra, in litt.).

[3]No specimen or photograph exists. Tentatively included on the basis of a statement in Grove and Lavenberg (1997:100) which states "the only record of a great hammerhead in the Archipelago is based on an observation along a vertical drop-off at Gordon Rocks at 30 m. Although rare within the islands, additional records can be expected."

RAJIDAE
GC *Bathyraja spinosissima* (Beebe & Tee-Van 1941)
P *Gurgesiella furvescens* de Buen 1959
EP *Raja velezi* Chirichigno 1973
G *Rajella eisenhardti* Long & McCosker 1999

DASYATIDAE
G? *Dasyatis* sp.
EP *Dasyatis brevis* (Garman 1879)
IP *Dasyatis dipterura* (Jordan & Gilbert 1880)
EP *Dasyatis longa* (Garman 1880)
EP *Himantura pacifica* (Beebe & Tee-Van 1941)
W *Pteroplatytrygon violacea* (Bonaparte 1832)
IP *Taeniura meyeni* Müller & Henle 1841

MYLIOBATIDAE
W *Aetobatus narinari* (Euphrasen 1790)
C *Myliobatis peruvianus* Garman 1913
EP *Pteromylaeus asperrimus* (Gilbert 1898)
EP *Rhinoptera steindachneri* Evermann & Jenkins 1891

MOBULIDAE
W *Manta birostris* (Walbaum 1792)
W *Mobula tarapacana* (Philippi 1892)
W *Mobula japanica* (Müller & Henle 1841)
EP *Mobula munkiana* Notabartolo-di-Sciara 1987

ELOPIDAE
EP *Elops affinis* Regan 1909

ALBULIDAE
EP *Albula esuncula* (Garman 1899)

HALOSAURIDAE
G *Halosaurus attenatus* Garman 1899

ANGUILLIDAE
IP(V) *Anguilla marmorata* Quoy & Gaimard 1824

CHLOPSIDAE
G *Chlopsis bicollaris* (Myers & Wade 1941)

MYROCONGRIDAE
EP *Myroconger nigrodentatus* Castle & Béarez 1995

MURAENIDAE
EP *Anarchias galapagensis* (Seale 1940)
EP *Echidna nocturna* (Cope 1872)
IP(V?) *Echidna nebulosa* (Ahl 1789)
IP(V) *Enchelycore lichenosa* (Jordan & Snyder 1901)
EP *Enchelycore octaviana* (Myers & Wade 1941)
IP *Gymnomuraena zebra* (Shaw 1797)
EP *Gymnothorax angusticeps* (Hildebrand & Barton 1949)
IP(V?) *Gymnothorax buroensis* (Bleeker 1857)
EP *Gymnothorax castaneus* (Jordan & Gilbert 1882)
EP *Gymnothorax dovii* (Günther 1870)
IP(V?) *Gymnothorax flavimarginatus* (Rüppell 1828)
IP(V) *Gymnothorax javanicus* (Bleeker 1859)
IP(V) *Gymnothorax meleagris* (Shaw & Nodder 1795)
EP *Gymnothorax panamensis* (Steindachner 1876)
IP(V?) *Gymnothorax pictus* (Ahl 1789)
EP *Muraena argus* (Steindachner 1870)
EP *Muraena clepsydra* Gilbert 1898
EP *Muraena lentiginosa* Jenyns 1842
IP *Scuticaria tigrina* (Lesson 1828)
IP *Uropterygius macrocephalus* (Bleeker 1864)
EP *Uropterygius polystictus* Myers & Wade 1941
EP *Uropterygius versutus* Bussing 1991

OPHICHTHIDAE
EP *Apterichtus equatorialis* (Myers & Wade 1941)
G *Callechelys galapagensis* McCosker & Rosenblatt 1972
EP *Herpetoichthys fossatus* (Myers & Wade 1941)
EP *Ichthyapus selachops* (Jordan & Gilbert 1882)
EP *Myrichthys xysturus* (Jordan & Gilbert 1882)
G *Ophichthus arneutes* McCosker & Rosenblatt 1998
GC *Ophichthus rugifer* Jordan & Bollman 1890
GCR *Paraletharchus opercularis* (Myers & Wade 1941)
EP *Phaenomonas pinnata* Myers & Wade 1941
GC *Quassiremus evionthas* (Jordan & Bollman 1890)[4]
EP *Scytalichthys miurus* (Jordan & Gilbert 1882)

CONGRIDAE
EP *Ariosoma gilberti* (Ogilby 1898)[5]
G *Bathycongrus* sp.
EP *Chiloconger dentatus* (Garman 1899)
EP *Gnathophis cinctus* (Garman 1899)
GC *Heteroconger klausewitzi* (Eibl-Eibesfeldt & Köster 1983)

[4]We consider *Leptocephalus alternatus* Fowler 1938:21 (from Tagus Cove, with 152 myomeres), to be a junior synonym of *Quassiremus evionthas*, which has 149-153 vertebrae.

[5]Eastern Pacific *Ariosoma* comprise a Mexican species, *A. hemiaspidus* (Wade 1946), and *A. gilberti*, known from Galápagos and Panama (D.G. Smith, in litt. 20 April 2009).

EP *Ophisoma prorigerum* Gilbert 1891[6]
C *Ophisoma* sp.
EP *Paraconger californiensis* Kanazawa 1961
EP *Paraconger similis* (Wade 1946)
EP *Xenomystax atrarius* Gilbert 1891

NETTASTOMATIDAE
EP *Facciolella equatorialis* (Gilbert 1891)

ENGRAULIDAE
EP *Anchoa ischana* (Jordan & Gilbert 1882)
EP *Anchoviella miarcha* (Jordan & Gilbert 1881)
EP *Cetengraulis mysticetus* (Günther 1866)
PC *Engraulis ringens* Jenyns 1842

CLUPEIDAE
W *Etrumeus teres* (DeKay 1842)
EP *Harengula thrissina peruana* (Fowler & Bean 1923)
EP *Lile stolifera* (Jordan & Gilbert 1882)
G *Opisthonema berlangai* Berry & Barrett 1964
EP *Opisthonema libertate* (Günther 1887)
PC *Sardinops sagax sagax* (Jenyns 1842)

CHANIDAE
IP *Chanos chanos* (Forsskål 1775)

ARGENTINIDAE
EP *Argentina aliceae* Cohen & Atsaides 1969

ATELEOPODIDAE
EP/EA *Guentherus altivela* Osorio 1917

ALEPOCEPHALIDAE
W *Bathytroctes macrolepis* Günther 1867
W *Narcetes erimelas* Alcock 1890

AULOPIDAE
G/C *Aulopus* sp.[7]

IPNOPIDAE
EP *Bathypterois atricolor* Alcock 1896
IP *Ipnops agassizii* Garman 1899

SYNODONTIDAE
EP *Synodus lacertinus* Gilbert 1890
EP *Synodus scituliceps* Jordan & Gilbert 1882

CHLOROPHTHALMIDAE
EP *Chlorophthalmus mento* Garman 1899

TRACHIPTERIDAE
W *Zu cristatus* (Bonelli 1819)

BREGMACEROTIDAE
W *Bregmaceros mcclellandi* Thompson 1840

MACROURIDAE
EP *Caelorinchus canus* (Garman 1899)
EP *Coryphaenoides anguliceps* (Garman 1899)
EP *Coryphaenoides armatus* (Hector 1875)
EP *Coryphaenoides boops* (Garman 1899)
PC *Coryphaenoides bucephalus* (Garman 1899)
EP *Coryphaenoides bulbiceps* (Garman 1899)
PC *Coryphaenoides delsolari* Chirichigno & Iwamoto 1977
G *Coryphaenoides gypsochilus* Iwamoto & McCosker 2001
G *Coryphaenoides myersi* Iwamoto & Sazanov 1988
EP *Mataeocephalus tenuicauda* (Garman 1899)
EP *Nezumia convergens* (Garman 1899)
G *Nezumia loricata loricata* Iwamoto 1979
EP *Nezumia stelgidolepis* (Gilbert 1890)
G *Nezumia ventralis* Hubbs & Iwamoto 1979
PC *Trachyrincus helolepis* Gilbert 1892

MORIDAE
W *Antimora rostrata* (Günther 1878)[8]
PC *Gadella filifer* (Garman 1899)
G *Gadella thysthlon* Long & McCosker 1998
EP *Laemonema gracillipes* Garman 1899
EP *Physiculus nematopus* Gilbert 1890

MERLUCIIDAE
PC *Merluccius gayi* (Guichenot 1848)-

CARAPIDAE
EP *Echiodon exsilium* Rosenblatt 1961
IP *Encheliophis vermicularis* Müller 1842
EP *Carapus dubius* (Putnam 1874)

OPHIDIIDAE
PC *Brotula ordwayi* Hildebrand & Barton 1949
IP *Bythonus caudalis* (Garman 1899)
EP *Cataetyx simus* Garman 1899
PC *Dicrolene nigra* Garman 1899

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[6]This deepwater (380-740 m) species belongs in a different, yet-to-be determined genus, *cf.* D. Smith (*in litt.*, 2009).

[7]Thompson (1998) initially recognized Galápagos and Cocos specimens as *Aulopus bajacali* Parin & Kotlyar 1984, but subsequently determined that they were a distinct species (pers. comm., July 1999). In 1999 he designated CAS Galápagos specimens as the holotype and paratypes but his description was never published.

[8]Photographed at numerous Galápagos localities from the submersible.

IP *Eretmichthys pinnatus* Garman 1899
EP *Monomitopus malispinosus* (Garman 1899)
EP *Otophidium indefatigabile* Jordan & Bollman 1890
EP *Petrotyx hopkinsi* Heller & Snodgrass 1903

BYTHITIDAE
G *Calamopteryx jeb* Cohen 1973
EP *Diplacanthopoma jordani* Garman 1899
EP *Grammonus diagrammus* (Heller & Snodgrass 1903)
G *Lucifuga inopinatus* Cohen & McCosker 1998
G *Ogilbia deroyi* (Poll & Van Mol 1966)
G *Ogilbia galapagosensis* (Poll & Leleup 1965)
G *Pseudonus acutus* Garman 1899

BATRACHOIDIDAE
EP *Porichthys margaritatus* (Richardson 1844)

LOPHIIDAE[9]
EP *Lophiodon spilurus* (Garman 1899)

ANTENNARIIDAE
EP *Antennarius avalonis* Jordan & Starks 1907
IP *Antennarius coccineus* (Cuvier 1831)
EP *Antennarius sanguineus* (Gill 1863)
EP *Antennatus strigatus* (Gill 1862)

OGCOCEPHALIDAE
G *Dibranchus crascens* Bradbury, McCosker & Long 1998
G *Dibranchus discors* Bradbury, McCosker & Long 1998
GC *Dibranchus erinaceus* (Garman 1899)
EP *Dibranchus hystrix* Garman 1899
G *Halieutopsis tumifrons* Garman 1899
PC *Ogcocephalus darwini* Hubbs 1952

MUGILIDAE
EP/A *Agonostomus monticola* (Bancroft 1834)
EP *Chaenomugil proboscidens* (Günther 1861)
W *Mugil cephalus* Linnaeus 1758
EP/A *Mugil curema* (Cuvier & Valenciennes 1836)
EP *Mugil thoburni* (Jordan & Starks 1896)

ATHERINIDAE
EP *Atherinella nesiotes* (Myers & Wade 1942)
EP *Melanorhinus cyanellus* (Meek & Hildebrand 1923)

EXOCOETIDAE
IP *Cheilopogon atrisignis* (Jenkins 1904)
IP *Cheilopogon dorsomacula* (Fowler 1944)
W *Cheilopogon furcatus* (Mitchell 1815)
IP *Cheilopogon spilonotopterus* (Bleeker 1866)
EP *Cheilopogon xenopterus* (Gilbert 1890)
EP *Cypselurus callopterus* (Günther 1866)
IP *Exocetus monocirrhus* Richardson 1846
W *Exocetus volitans* Linnaeus 1758
EP *Fodiator acutus rostratus* (Günther 1866)
EP *Hirundichthys marginatus* (Nichols & Breder 1928)
W *Hirundichthys rondeletii* (Valenciennes 1846)
W *Hirundichthys speculiger* (Valenciennes 1846)
IP *Prognichthys sealei* Abe 1955
IP *Prognichthys tringa* Breder 1828

HEMIRAMPHIDAE
IP *Euleptorhamphus viridis* (van Hasselt 1823)
EP *Hemiramphus saltator* Gilbert & Starks 1904
EP *Hyporhamphus gilli* Meek & Hildebrand 1923
EP *Hyporhamphus naos* Banford & Collette 2001
EP *Hyporhamphus snyderi* Banford & Collette 2001
W *Oxyporhamphus micropterus micropterus* (Valenciennes 1847)

BELONIDAE
W *Ablennes hians* (Valenciennes 1846)
EP *Platybelone argalus pterura* (Osburn & Nichols 1916)
EP *Strongylura exilis* (Girard 1854)
EP *Tylosurus crocodilus fodiator* Jordan & Gilbert 1882
EP *Tylosurus pacificus* (Steindachner 1876)

TRACHICHTHYIDAE
G *Hoplostethus pacificus* Garman 1899

HOLOCENTRIDAE
IP *Myripristis berndti* Jordan & Evermann 1903
EP *Myripristis leiognathus* Valenciennes 1846
EP *Sargocentron suborbitalis* (Gill 1864)

SYNGNATHIDAE
EP *Bryx veleronis* Herald 1940
EP *Cosmocampus arctus coccineus* (Herald 1940)
IP *Doryrhamphus excisus excisus* Kaup 1856
EP *Hippocampus ingens* Girard 1858

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[9]*Lophiodon caulinaris* (Garman's SU 1859 "Albatross" specimen was labeled Galápagos, and was published as *L. setigerus* by Gilbert 1891:454. It however is from the Gulf of Panama and not the Galápagos. Also note that *Chaunax latipunctatus* Le Danois (1984:96) is from Nazsca Ridge, not the Galápagos.

AULOSTOMATIDAE
IP *Aulostomus chinensis* (Linnaues 1766)

FISTULARIIDAE
IP *Fistularia commersonii* Rüppell 1835
EP *Fistularia coroneta* Gilbert & Starks 1904

SCORPAENIDAE
W *Ectreposebastes imus* Garman 1899
G *Idiastion hageyi* McCosker 2008
G *Phenacoscorpius* sp.
EP *Pontinus clemensi* Fitch 1955
GC *Pontinus strigatus* Heller & Snodgrass 1903
EP *Pontinus vaughani* Barnhart & Hubbs 1946
GC? *Pontinus* sp. A Poss & Lavenberg in prep.
EP *Pontinus* sp. B Poss & Lavenberg in prep.
G *Pontinus* sp. C Poss in prep.
EP *Scorpaena histrio* Jenyns 1840
EP *Scorpaena mystes* Jordan & Starks 1895
GC *Scorpaena cocosensis* Motomura 2004
GC *Scorpaenodes rubrivinctus* Poss, McCosker & Baldwin 2010
EP *Scorpaenodes xyris* (Jordan & Gilbert 1882)
IP(V) *Taenianotus triacanthus* Lacepède 1802
G *Trachyscorpia osheri* McCosker 2008

TRIGLIDAE
G *Bellator farrago* Richards & McCosker 1998
EP *Peristidion crustosum* (Garman 1899)
G *Prionotus miles* Jenyns 1840
EP *Prionotus stephanophrys* Lockington 1881

LIPARIDAE
G *Paraliparis darwini* Stein & Chernova 2002
G *Paraliparis galapagosensis* Stein & Chernova 2002

CENTROPOMIDAE
EP *Centropomus viridis* Lockington 1887

SERRANIDAE[10]
EP *Alphestes immaculatus* Breder 1936
EP *Anthias noeli* Anderson & Baldwin 2000
EP *Cephalopholis panamensis* (Steindachner 1876)
C *Cratinus agassizii* Steindachner 1878
EP *Dermatolepis dermatolepis* (Boulenger 1895)
EP *Diplectrum eumelum* Rosenblatt & Johnson 1974
EP *Diplectrum euryplectrum* Jordan & Bollman 1890
EP *Diplectrum macropoma* (Günther 1864)
EP *Diplectrum rostrum* Bortone 1974
EP *Epinephelus analogus* Gill 1864
EP *Epinephelus cifuentesi* Lavenberg & Grove 1993
EP *Epinephelus labriformis* (Jenyns 1840)
EP/A *Epinephelus mysticinus* (Poey 1852)
EP/A *Epinephelus niphobles* Gilbert & Starks 1897
EP *Hemianthias peruanus* (Steindachner 1874)
EP *Liopropoma fasciatum* Bussing 1980
EP *Liopropoma longilepis* Garman 1889
GCM *Mycteroperca olfax* (Jenyns 1840)
EP *Mycteroperca xenarcha* (Jordan 1881)
G *Paralabrax albomaculatus* (Jenyns 1840)
EP *Paranthias colonus* (Valenciennes 1855)
EP *Pronotogrammus multifasciatus* Gill 1863
EP *Pseudogramma thaumasium* (Gilbert 1900)
EP *Rypticus bicolor* Valenciennes 1846
EP *Rypticus nigripinnis* Gill 1861
EP *Serranus aequidens* Gilbert 1890
EP *Serranus psittacinus* Valenciennes 1855
G *Serranus stilbostigma* (Jordan & Bollman 1890)

INCERTAE SEDIS[11]
PC *Hemilutjanus macropthalmus* (Tschudi 1845)

OPISTOGNATHIDAE
G *Opistognathus galapagensis* Allen & Robertson 1991

PRIACANTHIDAE
W *Cookeolus japonicus* (Cuvier 1829)
W *Heteropriacanthus cruentatus* (Lacepède 1801)
EP *Pristigenys serrula* (Gilbert 1891)
IP *Priacanthus cf. meeki* Jenkins 1903

APOGONIDAE
GCM *Apogon atradorsatus* Heller & Snodgrass 1903
EP *Apogon dovii* Günther 1861
EP *Apogon pacifici* (Herre 1935)
EP *Howella pammelas* (Heller & Snodgrass 1903)

EPIGONIDAE
G *Epigonus merleni* McCosker & Long 1997

MALACANTHIDAE
EP *Caulolatilus affinis* Gill 1865
EP *Caulolatilus princeps* (Jenyns 1840)
IP *Malacanthus brevirostris* Guichenot 1848

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[10]Kuiter (2004:116) lists the distribution of *Hypoplectrodes semicinctus* as "Juan Fernández Islands, where common, rare in the Galápagos Islands and a single record from Easter Island." We are unaware of any specimen from Galápagos or of any other published record.

[11]Not a serranid, as other authors have recently suggested (*cf.* G. David Johnson, in litt.).

NEMATISTIIDAE
EP *Nematistius pectoralis* Gill 1862

CORYPHAENIDAE
W *Coryphaena equiselis* Linnaeus 1758
W *Coryphaena hippurus* Linnaeus 1758

ECHENEIDAE
W *Echeneis naucrates* Linnaeus 1758
W *Phtheirichthys lineatus* (Menzies 1791)
W *Remora brachyptera* (Lowe 1839)
W *Remora osteochir* (Cuvier 1829)
W *Remora remora* (Linnaeus 1758)
W *Remorina albescens* (Temminck & Schlegel 1845)

CARANGIDAE[12]
IP *Alectis ciliaris* (Bloch 1787)
IP *Caranx caballus* Günther 1868
EP *Caranx caninus* Günther 1867
W *Caranx lugubris* Poey 1860
IP *Caranx melampygus* Cuvier 1833
IP *Caranx orthogrammus* (Jordan & Gilbert 1882)
EP *Caranx otrynter* Jordan & Gilbert 1883
IP *Caranx sexfasciatus* Quoy & Gaimard 1825
IP *Decapterus macrosoma* Bleeker 1851
EP *Decapterus muroadsi* (Temminck & Schlegel 1844)
W *Elegatis bipinnulata* (Quoy & Gaimard 1825)
IP *Gnathanodon speciosus* (Forsskål 1775)
W *Naucrates ductor* (Linnaeus 1758)
EP *Oligoplites saurus* (Bloch & Schneider 1801)
W *Selar crumenophthalmus* (Bloch 1793)
EP *Selene peruviana* (Guichenot 1866)
W *Seriola lalandi* Valenciennes 1833
W *Seriola rivoliana* Valenciennes 1833
EP *Trachinotus paitensis* Cuvier 1832
EP *Trachinotus rhodopus* Gill 1863
EP *Trachinotus stilbe* (Jordan & McGregor 1898)
IP/C *Trachurus murphyi* Nichols 1920
W *Uraspis helvola* (Forster 1801)

LUTJANIDAE
EP *Hoplopagrus guentheri* Gill 1862
EP *Lutjanus aratus* (Günther 1864)
EP *Lutjanus argentiventris* (Peters 1869)
EP *Lutjanus guttatus* (Steindachner 1869)
EP *Lutjanus jordani* (Gilbert 1898)
EP *Lutjanus novemfasciatus* (Gill 1862)
EP *Lutjanus viridis* (Valenciennes 1846)
IP(V) *Pristipomoides zonatus* (Valenciennes 1830)

BRAMIDAE
W *Brama dussumieri* Cuvier 1831
P/A *Taractes rubescens* (Jordan & Evermann 1887)

GERRIIDAE
EP *Diapterus peruvianus* (Cuvier 1830)
EP/A *Eucinostomus argenteus* Baird & Girard 1855
EP *Eucinostomus currani* Zahuranec 1980
EP *Eucinostomus dowii* (Gill 1863)
EP *Eucinostomus gracilis* (Gill 1862)
EP *Eugerres lineatus* (Humboldt 1821)
EP/A *Gerres cinereus* (Walbaum 1792)

HAEMULIDAE
EP *Anisotremus interruptus* (Gill 1862)
P *Anisotremus scapularis* (Tschudi 1845)
EP *Haemulon scudderii* Gill 1862
EP *Haemulon sexfasciatum* Gill 1862
G *Orthopristis cantharinus* (Jenyns 1840)
EP *Orthopristis chalceus* (Günther 1864)
G *Orthopristis forbesi* Jordan & Starks 1897
G *Orthopristis lethopristis* Jordan & Fesler 1889
G *Xenichthys agassizi* Steindachner 1875
EP *Xenichthys xanti* Gill 1863
G *Xenocys jessiae* Jordan & Bollmann 1890

SPARIDAE
G *Archosargus pourtalesii* (Steindachner 1881)
EP *Calamus brachysomus* (Lockington 1880)
EP *Calamus taurinus* (Jenyns 1840)

POLYNEMIDAE
EP *Polydactylus approximans* (Lay & Bennett 1839)

SCIAENIDAE
P *Cilus gilberti* (Abbott 1899)
EP *Corvula macrops* (Steindachner 1875)
EP *Cynoscion phoxocephalus* Jordan & Gilbert 1882
EP *Larimus pacificus* Jordan & Bollman 1890
G *Odontoscion eurymesops* (Heller & Snodgrass 1903)
G *Pareques perissa* (Heller & Snodgrass 1903)
G *Umbrina galapagorum* Steindachner 1878

[12]*Decapterus macarellus* (Cuvier 1833) has been listed from the Galápagos by recent authors. Grove and Lavenberg's (1997) confusing and inconsistent treatment of this species is explained by McCosker (1998:810) and by Baldwin (1998:584). We tentatively exclude it from our listing based on the advice of W.F. Smith-Vaniz (in litt. 19 Feb. 1998) who wrote "I am virtually certain that I have seen no specimens of *Decapterus macarellus* from the Galapagos (although it possibly occurs there) ... Small individuals of *D. muroadsi* are difficult to distinguish from *D. macarellus*, and I have examined museum collections of that species and *D. macrosoma* that were identified as *D. macarellus*."

MULLIDAE
EP *Mulloidichthys dentatus* (Gill 1862)
EP *Pseudupeneus grandisquamis* (Gill 1863)

KYPHOSIDAE
G *Girella fremenvillei* (Valenciennes 1846)
EP *Kyphosus analogus* (Gill 1862)
EP *Kyphosus elegans* (Peters 1869)
IP *Sectator ocyurus* (Jordan & Gilbert 1881)

CHAETODONTIDAE
IP(V) *Chaetodon auriga* Forsskål 1775
EP *Chaetodon humeralis* Günther 1860
IP(V) *Chaetodon kleinii* Bloch 1790
IP(V) *Chaetodon lunula* (Lacepède 1803)
IP(V) *Chaetodon meyeri* Bloch & Schneider 1801
IP(V) *Chaetodon unimaculatus* Bloch 1787
IP *Forcipiger flavissimus* Jordan & McGregor 1898
EP *Johnrandallia nigrirostris* (Gill 1862)
EP *Prognathodes falcifer* (Hubbs & Rechnitzer 1958)[13]

POMACANTHIDAE
EP *Holacanthus passer* Valenciennes 1846
EP *Pomacanthus zonipectis* (Gill 1862)

KUHLIIDAE
IP *Kuhlia mugil* (Forster 1801)

OPLEGNATHIDAE
PC *Oplegnathus insignis* (Kner 1867)

CIRRHITIDAE
IP *Cirrhitichthys oxycephalus* (Bleeker 1855)
EP *Cirrhitus rivulatus* (Valenciennes 1846)
IP *Oxycirrhites typus* Bleeker 1857

CICHLIDAE
Introduced *Oreochromis mossambicus* (Peters 1852)

POMACENTRIDAE
EP *Abudefduf concolor* (Gill 1862)
EP *Abudefduf troschelii* (Gill 1862)
G *Azurina eupalama* Heller & Snodgrass 1903
EP *Chromis alta* Greenfield & Woods 1980
EP *Chromis atrilobata* Gill 1862
EP *Microspathodon bairdi* (Gill 1862)
EP *Microspathodon dorsalis* (Gill 1862)
P *Nexilosus latifrons* (Tschudi 1845)
EP *Stegastes acapulcoensis* (Fowler 1944)
EP *Stegastes arcifrons* (Heller & Snodgrass 1903)
GCM *Stegastes beebei* (Nichols 1924)
EP *Stegastes flavilatus* (Gill 1862)

LABRIDAE
EP *Bodianus diplotaenia* (Gill 1862)
P *Bodianus eclancheri* (Valenciennes 1855)
EP *Decodon melasma* Gomon 1974
GC *Halichoeres adustus* (Gilbert 1890)
EP *Halichoeres chierchiae* Caporiacco 1947
EP *Halichoeres dispilus* (Günther 1864)
EP *Halichoeres melanotis* (Gilbert 1890)
EP *Halichoeres nicholsi* (Jordan & Gilbert 1881)
EP *Halichoeres notospilus* (Günther 1864)
GC *Halichoeres raisneri* Baldwin & McCosker 2001
IP *Iniistius pavo* (Valenciennes 1840)
IP *Novaculichthys taeniourus* (Lacepède 1801)
C *Semicossyphus darwini* (Jenyns 1842)
IP *Stethojulis bandanensis* (Bleeker 1851)
IP *Thalassoma grammaticum* Gilbert 1890
EP *Thalassoma lucasanum* (Gill 1862)
IP *Thalassoma purpureum* (Forsskål 1775)
GC *Xyrichtys victori* Wellington 1992
G *Xyrichtys* sp.

SCARIDAE
IP *Calotomus carolinus* (Valenciennes 1840)
EP *Nicholsina denticulata* (Evermann & Radcliffe 1917)
EP *Scarus compressus* (Osborn & Nichols 1916)
IP *Scarus ghobban* Forsskål 1775
EP *Scarus perrico* (Jordan & Gilbert 1881)
IP *Scarus rubroviolaceus* Bleeker 1847

ZOARCIDAE
AP *Lycodapus australis* Norman 1937
EP *Melanostigma bathium* Bussing 1965
EP *Thermarces cerberus* Rosenblatt & Cohen 1986

AMMODYTIDAE
EP *Ammodytoides gilli* (Bean 1895)

URANOSCOPIDAE
EP *Kathetostoma averruncus* Jordan & Bollman 1890

TRIPTERYGIIDAE
G *Lepidonectes corallicola* (Kendall & Radcliffe 1912)

DACTYLOSCOPIDAE
G *Dactyloscopus lacteus* (Myers & Wade 1946)
EP *Gillelus semicinctus* Gilbert 1890
G *Myxodagnus sagitta* Myers & Wade 1946
G *Platygillelus rubellulus* (Kendall & Radcliffe 1912)

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[13]We consider *Prognathodes carlhubbsi* Nalbant 1995 to be a junior synonym of *P. falcifer*.

BLENNIIDAE
EP *Entomacrodus chiostictus* (Jordan & Gilbert 1882)
EP *Hypsoblennius brevipinnis* (Günther 1861)
EP *Ophioblennius steindachneri* Jordan & Evermann 1898
EP *Plagiotremus azaleus* (Jordan & Bollman 1890)

LABRISOMIDAE
G *Cottoclinus canops* McCosker, Stephens & Rosenblatt 2003
GC *Dialommus fuscus* (Gilbert 1891)
GM *Labrisomus dendriticus* (Reid 1935)
G *Labrisomus jenkinsi* (Heller & Snodgrass 1903)
EP *Labrisomus multiporosus* Hubbs 1953
EP *Malacoctenus tetranemus* (Cope 1877)
G *Malacoctenus zonogaster* Heller & Snodgrass 1903
G *Starksia galapagensis* Rosenblatt & Taylor 1971

CHAENOPSIDAE
G *Acanthemblemaria castroi* Stephens & Hobson 1966
G *Chaenopsis schmitti* Böhlke 1957
G *Ekemblemaria* sp.[14]

GOBIESOCIDAE
GC *Arcos poecilophthalmus* (Jenyns 1842)
C *Tomicodon chilensis* Brisout de Barnesville 1846
EP *Tomicodon petersi* (Garman 1875)

CALLIONYMIDAE
EP *Synchiropus atrilabiatus* (Garman 1899)

ELEOTRIDAE
EP *Dormitator latifrons* (Richardson 1844)
G *Eleotrica cableae* Ginsburg 1933
EP *Eleotris picta* Kner & Steindachner 1863
EP *Gobiomorus maculatus* (Günther 1859)

GOBIIDAE
G *Bathygobius lineatus lineatus* Jenyns 1841
G *Chriolepis tagus* Ginsburg 1953
EP *Coryphopterus urospilus* Ginsburg 1938
GC *Elecatinus nesiotes* Bussing 1990
EP *Lythrypnus dalli* (Gilbert 1890)
G *Lythrypnus gilberti* (Heller & Snodgrass 1903)
GCMR *Lythrypnus rhizophora* (Heller & Snodgrass 1903)

MICRODESMIDAE
EP *Clarkichthys bilineatus* (Clark 1936)
EP *Microdesmus dipus* Günther 1864

EPHIPPIDAE
EP *Chaetodipterus zonatus* (Girard 1858)

LUVARIDAE
W *Luvarus imperialis* Rafinesque 1810

ZANCLIDAE
IP *Zanclus cornutus* (Linnaeus 1758)

ACANTHURIDAE
IP *Acanthurus nigricans* (Linnaeus 1758)
IP *Acanthurus triostegus triostegus* (Linnaeus 1758)
IP *Acanthurus xanthopterus* Valenciennes 1835
IP(V) *Naso brevirostris* (Cuvier 1829)
IP(V) *Naso vlamingii* (Valenciennes 1835)
EP *Prionurus laticlavius* (Valenciennes 1846)

SPHYRAENIDAE
W(V) *Sphyraena barracuda* (Walbaum 1792)
P *Sphyraena idiastes* Heller & Snodgrass 1903

GEMPYLIDAE
W *Gempylus serpens* Cuvier 1829
W *Lepidocybium flavobrunneum* (Smith 1849)
W *Nealotus tripes* Johnson 1865
W *Ruvettus pretiosus* Cocco 1823

TRICHIURIDAE
IP *Aphanopus capricornis* Parin 1994
W *Benthodesmus tenuis* (Günther 1877)
G *Lepidopus manis* Rosenblatt & Wilson 1987
EP *Trichiurus nitens* Garman 1899

SCOMBRIDAE
W *Acanthocybium solandri* (Cuvier 1831)
EP *Auxis rochei eudorax* Collette & Aadland 1996
EP *Auxis thazard brachydorax* Collette & Aadland 1996
IP *Euthynnus lineatus* Kishinouye 1920
W *Katsuwonus pelamis* (Linnaeus 1758)
IP *Sarda orientalis* (Temminck & Schlegel 1844)
IP *Scomber japonicus* Hottuyn 1782
EP *Scomberomerus sierra* Jordan & Starks 1895
W *Thunnus alalunga* (Bonnaterre 1788)
W *Thunnus albacares* (Bonnaterre 1788)
W *Thunnus obesus* (Lowe 1839)

XIPHIIDAE
W *Xiphias gladius* Linnaeus 1758

[13]Still an uncollected species, seen and photographed at Plazas Island (McCosker et al. 1978).

ISTIOPHORIDAE
IP *Istiophorus platypterus* (Shaw & Nodder 1792)
W *Makaira indica* (Cuvier 1832)
W *Makaira mazara* (Jordan & Snyder 1901)
W *Tetrapterus angustirostris* Tanaka 1915
IP *Tetrapterus audax* (Philippi 1887)

CENTROLOPHIDAE
C *Seriolella violacea* Guichenot 1848

NOMEIDAE
W *Cubiceps pauciradiatus* Günther 1872
W *Nomeus gronovii* (Gmelin 1788)
W *Psenes arafurensis* Günther 1889
W *Psenes cyanophrys* Valenciennes 1833
W *Psenes pellucidus* Lütken 1880
EP *Psenes sio* Haedrich 1970

STROMATEIDAE
EP *Peprilus medius* (Peters 1869)

PARALICHTHYIDAE
G *Citharichthys gnathus* Hoshino & Amaoka 1999
EP *Hippoglossina bollmani* Gilbert 1890
EP *Paralichthys woolmani* Jordan & Williams 1897

BOTHIDAE
EP *Bothus leopardinus* (Günther 1862)
IP *Bothus mancus* (Broussonet 1782)
EP *Monolene maculipinna* Garman 1899
EP *Syacium ovale* (Günther 1864)

ACHIRIDAE
EP *Aseraggodes herrei* Seale 1940
EP *Trinectes fonsecensis* (Günther 1862)

CYNOGLOSSIDAE
EP *Symphurus atramentatus* Jordan & Bollman 1890
G *Symphurus diabolicus* Mahadeva & Munroe 1990
EP *Symphurus varius* Garman 1899

BALISTIDAE
IP *Balistes polylepis* Steindachner 1876[15]
W *Canthidermis maculatus* (Bloch 1786)
W *Melichthys niger* (Bloch 1786)
IP *Melichthys vidua* (Solander 1844)
EP *Pseudobalistes naufragium* (Jordan & Starks 1895)
EP *Sufflamen verres* (Gilbert & Starks 1904)
IP(V?) *Xanthichthys caeruleolineatus* Randall, Matsuura & Zana 1978
IP *Xanthichthys mento* (Jordan & Gilbert 1882)

MONACANTHIDAE
W *Aluterus monocerus* (Linnaeus 1758)
W *Aluterus sriptus* (Osbeck 1765)
IP *Cantherhinus dumerilii* (Hollard 1854)

OSTRACIIDAE[16]
W Ostracion meleagris Shaw 1796

TETRAODONTIDAE
IP *Arothron hispidus* (Linnaeus 1758)
IP *Arothron meleagris* (Bloch & Schneider 1801)
IP *Arothron nigropunctatus* (Bloch & Schneider 1801)
IP(V) *Canthigaster amboinensis* (Bleeker 1865)
IP(V) *Canthigaster janthinoptera* (Bleeker 1855)
EP *Canthigaster punctatissima* (Günther 1870)
IP(V) *Canthigaster valentini* (Bleeker 1853)
W *Lagocephalus lagocephalus* (Linnaeus 1758)
G *Sphoeroides angusticeps* (Jenyns 1842)
EP *Sphoeroides annulatus* (Jenyns 1842)
EP *Sphoeroides lobatus* (Steindachner 1870)

DIODONTIDAE
W *Chilomycterus reticulatus* (Linnaeus 1758)
IP(V) *Cyclichthys spilostylus* (Leis & Randall 1982)
W *Diodon eydouxii* Brisout de Barneville 1846
W *Diodon holocanthus* Linnaeus 1758
W *Diodon hystrix* Linnaeus 1758

MOLIDAE
W *Masturus lanceolatus* (Liénard 1840)
W *Mola mola* (Linnaeus 1758)
W *Ranzania laevis* (Pennant 1776)

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[15]Widespread in the eastern Pacific from northern California to Peru, and also in Hawaii (Randall & Mundy 1998) and one individual from the Marquesas (Randall & Earle 2000).

[16]*Lactoria diaphana* (Bloch & Schneider 1801), was listed in Thomson et al. (1979:238) as from Galápagos. Although widespread in distribution, it is not included in that no specimen exists and no individual has been reported as yet.

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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Collecting Evolution: The Vindication of Charles Darwin by the 1905-1906 Galápagos Expedition of the California Academy of Sciences

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For 17 months, from June 1905 to November 1906, the California Academy of Sciences in San Francisco sent out an expedition of "eight young men" on the 89-foot schooner *Academy*, lead by Rollo Howard Beck. The expedition took three months to reach the Galápagos , having stopped at a series of Mexican islands and Isla Cocos on the way south, then spent a year and a day collecting on all the major and minor islands in the Galápagos, and returned home non-stop by sailing for two months. During this expedition, the longest in Galápagos expedition history, some 75,000 specimens were collected. Today, these well-curated specimens housed at the California Academy of Sciences form an important historical baseline for conservation efforts by the Charles Darwin Foundation, Galápagos National Park Service, and Academy researchers. Species that were common 100 years ago might be rare or endangered today, such as the Mangrove Finch, Flightless Cormorant, and Galápagos Penguin. A key to the success of the 1905–06 expedition was that each of the eight young men had their own scientific collecting specialty: birds, reptiles, plants, insects, fossils, rocks, mammals, and seashells. During the 05–06 expedition there was a series of "firsts" for Galápagos : the first sighting of tool use by the Woodpecker Finch, the first (and only) tortoise from Fernandina Island, and the naming of Academy Bay. The specimens collected 70 years after Darwin visited in 1835 are actively used in evolutionary studies involving DNA samples, conservation efforts involving restoring plant and animal populations, and taxonomy and biogeography studies that examine how species distributions have changed over time. The enduring legacy of the 1905–06 expedition encompasses much of what we know about Galápagos today, including: giant tortoise taxonomy, David Lack's concept of "Darwin's Finches," and plant zonation from coast to highlands. This knowledge stems from the intrepid "eight young men" who explored and collected under difficult and dangerous conditions, and whose field work has allowed us to better understand what is commonly known as Darwin's living outdoor laboratory of evolution.

KEYWORDS: Galápagos Islands, Charles Darwin, conservation, Rollo Howard Beck, California Academy of Sciences, fieldwork, museum collection

When the schooner *Academy* sailed out of San Francisco Bay on June 28, 1905, her crew had a clear objective: collect scientific specimens for the largest natural history museum west of the Mississippi River, the California Academy of Sciences. The eleven members of the expedition consisted of a cadre of collectors, eight young men who served as sailor-scientists, plus a navigator, a mate, and a cook (Fig. 3). Together they traveled for 17 months to the Galápagos Islands and back,

returning on Thanksgiving night in 1906. Through their extensive collecting efforts that lasted a year and a day in the islands they brought the Galápagos back to San Francisco, in the form of some 75,000 specimens. And in the process they vindicated Charles Darwin many times over, which is the enduring legacy of their expedition. Today, Darwin's Finches perch prominently in the narrative and illustrations of every high school and college introductory biology textbook. These rightly famous birds were transformed from obscure "Galapagos Finches" into exemplary "Darwin's Finches" by taxonomic research on the museum specimens collected by the 1905–06 expedition and housed, securely to this day, at the Academy in Golden Gate Park in San Francisco.

The Galápagos Islands are well known for scientific visits by Charles Darwin in 1835 and William Beebe in the 1920s, but those important visits were eclipsed in duration and significance by the 1905-1906 expedition of the California Academy of Sciences. Darwin and Beebe inspired generations of scientists and colonists to converge on the Galápagos. Their popular books brought justified fame to the remote archipelago. Darwin's *Journal of Researches* (popularly known as *The Voyage of the Beagle*) and Beebe's two books *Galapagos — World's End* (1924) and *The* Arcturus *Adventure* (1926) motivated scientists, travelers, and European immigrants (for example, in the late 1920s to late 1930s from Germany, the infamous Frederich Ritter and Dore Straucher, and the multi-generational colonists Witmer and Angermeyer families) to make the Galápagos a scientific, personal and spiritual paradise.

Arguably though, Darwin, for all his justified fame, made a few mistakes with his interpretations of the giant tortoises and the finches, and Beebe was mainly an explorer and adventurer rather than a scientist. Their books are prominent to this day, still in print, and still widely read and influential. But the solid foundation of scientific collecting that mainstream zoologists and botanists still utilize today for Galápagos research was built by the 1905–06 expedition.

The 1905-06 Galápagos Islands expedition was the second major international expedition organized and financed by the California Academy of Sciences. However, its significance in the history of the archipelago transcends its vital role in the Academy's more than150-year history. It has proven to be, in the 100+ years since its celebrated departure from San Francisco in the summer of 1905, the longest and most extensive expedition in Galápagos history. The California Academy of Sciences is the West Coast's largest and oldest museum. The 1905–1906 Galápagos expedition is remembered now, through a quirk — or perhaps more accurately a fault — of history, as the foundation of the Academy's famous collections and research programs.

Motivation for the Expedition

Within the institutional history of the California Academy of Sciences, the organizers of this expedition were motivated by a desire to build up the size and taxonomic diversity of the scientific collections of the museum. Within the eight separate biographical trajectories of the expedition's field party, the expedition greatly influenced their subsequent personal and professional lives. This was particularly true for Rollo Howard Beck, who went on to become the premier bird collector of his day.[1] From a biological conservation perspective, the expedition collected a large number of specimens at a time when collecting regulations were not in place in the islands and they really had no other choice. For them, collecting *was* conservation, or at least the material would be safely preserved in San Francisco.

Founded in 1853, the Academy grew slowly in its early years and more rapidly in the years

[1] See Dumbacher, J.P. & West, B. 2010 (this volume). Collecting Galápagos and the Pacific: How Rollo Howard Beck Shaped Our Understanding of Evolution; Pitelka, F.A. 1986. Rollo Beck — Old-school collector, member of an endangered species. *American Birds* 40(3): 385–387.

following a substantial financial bequest from millionaire James Lick in 1875. The financial independence of the Academy was clearly established after receiving much-needed capital from the Lick Trust in the 1880s. After they had built a new museum building on the corner of 4th and Market Streets in 1891, they set their sights on increasing the size and significance of their research collections by expanding their field collecting operations. After some 50 years of existence, the Academy as an institution finally felt confident in flexing its academic and financial muscles and believed that "exploration would build up the collections and afford ample material for publications by the curators."[2]

Housing sizeable museum collections and publishing significant scholarly contributions served to further advertise the arrival on the scientific scene of the newly-solvent Academy and its dedicated curators. A museum needs a research collection, and the more extensive and substantial the better. The Lick bequest allowed them to build an impressive museum on Market Street in San Francisco, now they needed scientific expeditions to fill their otherwise empty wooden specimen cabinets.

After successfully struggling for scientific respect and legitimacy through the publication series called the *Proceedings*, the Academy now desired to catch up in other ways with older east coast museums in New York, Cambridge, Philadelphia, and elsewhere. Subscribing to an Edwardian version of the doctrine that 'you have to spend money to make money,' the Academy realized that investing new income in international exploration would "doubtless attract outside assistance to enlarge the work." The Academy intended to emulate the prestigious American Museum of Natural History in New York City and other institutions whose fieldwork placed them "in the vanguard of scientific institutions."[3]

The Academy started these field projects on a modest scale, as its conservative board of directors was inclined to do, and built momentum in the early years of the 20th century. Initially they undertook small-scale collecting trips involving a curator or principal field collector and a few field assistants. These early collecting trips focused primarily on California, and occasionally other western states. These mini-expeditions brought back specimens, usually limited to the curator's taxonomic specialty, and normally in modest quantities. But an ambitious museum like the Academy playing "catch-up ball" with the big eastern museums needed to take a quantum leap.

An exception to this early pattern was a series of five collecting trips between 1889 and 1894 to what was then called "Lower California," or today the Baja California peninsula in México.[4] Importantly, these trips served to expand the Academy's geographic horizons beyond the boundaries of the United States and to set the stage for longer, more extensive trips. The combination of institutional and personal ambition that propelled the Academy out of its provincial existence onto the international scene was manifest in its Director, Leverett Mills Loomis (1857–1928) (Fig. 1).

Loomis came to the Academy in May 1894 from South Carolina as a 36-year old curator of ornithology and went on to become Director from 1902 to 1912.[5] Loomis was at the helm during some of the most important years in Academy history. His scientific passion was sea birds, and in particular the group that includes albatrosses, shearwaters and petrels that share the unusual

[2] Hittell, T.H. 1997. The California Academy of Sciences — A Narrative History: 1853–1906, edited by A.E. Leviton & M.L. Aldrich. San Francisco, CA, p. 414.

[3] Hittell, op. cit., p. 414.

[4] Hittell, op. cit., p. 305 (1889 trip), p. 313 (1890 trip), p. 334 (1892 trip), p. 342 (1893 trip) and p. 348 (1894 trip). Specific details of these trips are scarce, due to the destruction of correspondence and official records in the April 18, 1906 earthquake and subsequent three days of fire that destroyed the California Academy of Sciences.

[5] Hittell, op. cit., p. 346 for first mention of Loomis; also, two obituaries of Loomis: T.S.P. [T.S. Palmer]. 1928, "Untitled obituary notice in News and Notes section", The Auk, Vol. 45, pp. 263–264; and, Bishop, L.B. 1929, In Memoriam: Leverett Mills Loomis. The Auk, vol. 46, pp. 1–13.

anatomical distinction of having tube-shaped nostrils. His interest in these tube-noses, or 'tubinares,' as they were called scientifically in Loomis' day (today they are reclassified as the less euphonious Procellariiformes), and his desire to build up one of the world's best collections of these birds, would result in Loomis forming a strong and lasting alliance with the premier collector of sea birds and expedition leader Rollo Howard Beck (1870–1950). Loomis was motivated by both an institutional agenda as well as a personal agenda for the 1905–06 expedition. Institutionally, the California Academy of Sciences desired through their governing board to build up their specimen collections to world-class standing, to publish the results of curator research, and to gain the respect of their sister institutions, such as the American Museum of Natural History in New York. Personally, Loomis desired a diverse collection of worldwide tube-nosed sea birds for his own scholarly work. These dual desires were manifest in the 1905–06 expedition.

FIGURE 1. Leverett Mills Loomis. (Courtesy California Academy of Sciences Archives [N21355].)

In addition, Loomis was aware that collecting in the Galápagos Islands was crucial "before it was too late," as reports were arriving, partly through Rollo Beck, that species of Galápagos tortoise had suffered tremendous depredations from historical and ongoing wholesale slaughter from the likes of by pirates, buccaneers, whalers, and other mariners, as well as residents of the islands. This additional motivation meant engaging in what amounted to salvage collecting, with the perspective that specimens were better dead and preserved in a museum collection (where they could be studied in perpetuity by scientists) than left to the vagaries and vicissitudes of unprotected life in the archipelago. This was clearly a decision historically necessitated by lack of any protective measures for the organisms, and a situation very different from today with the Galápagos National Park Service and the Charles Darwin Foundation operating on the forefront of conservation. The 1905–06 expedition must be viewed in this historical context, not by present day conservation standards. At the time, it was the right thing to do.

In January 1903, exactly a year after becoming Director, Loomis unveiled a bold plan that would shape the course of the Academy for years to come. Loomis wanted to move the Academy into the academic big league, and he planned to do so by going down to the sea in ships. "For the preceding year the work of the museum has been largely devoted to the housing and arrangement of scientific specimens," Loomis optimistically told the CAS Council, "but it is now in readiness for exploration and larger accessions."[6] As far as Loomis was concerned, the best places to acquire larger collections were the offshore islands of Mexico, and eventually the evolutionary Mecca of the Galápagos Islands.

Part of the Academy's institutional route to financial success and academic credibility lay in amassing large numbers of museum specimens. When it comes to museum collections, there is

[6] Hittell, op. cit., p. 412.

truth in the aphorism "Quantity has a quality all its own."[7] Loomis was acutely aware that as far as museum collections were concerned, size really did matter. He was also aware of the obverse of the aphorism, that "Quality has a quantity all its own," and sought to obtain the best and most diverse specimens through careful fieldwork and exchange for duplicate specimens. To this end, in early 1903, Loomis sought and received approval from the Board of Trustees to establish a $4,000 Exploration Fund "as a means of enlarging the scope of the Academy and building up its departments." Even today, the Academy describes itself accurately on its history web page as "one of the 10 largest natural history museums in the world."[8] On that same page, the Academy rightfully compares itself to its sister institutions "the Smithsonian Institution, the American Museum of Natural History in New York and the Field Museum in Chicago" as one of the nation's premier museums concerned with "the study, display and interpretation of scientific collections which inspire people of all ages to explore the rich variety of life on Earth." A concise current description of the Academy is: "Exploring, explaining and protecting the natural world. Since 1853." Fortunately for those concerned with natural history, nothing has changed in over 150 years. Loomis would be right at home with this description and goals of the modern California Academy of Sciences.

Connection to Darwin

Charles Darwin clearly knew what he was up against when he sat at his writing chair in the ground floor study of his country home, Down House, located 16 miles south of London, penning the first draft of *The Origin of Species*. Darwin sat in his study and wrote nearly daily for many months during 1858 and into 1859 with a big window to his left opening up to sweeping views of an extensive lawn, his brick and glass greenhouse for plant experiments, and the Sand Walk where he retreated daily for pensive, therapeutic strolls. Walking on that comfortable, level path, keeping track of the number of loops he walked by kicking aside black chert cobbles, Darwin knew he was fighting an uphill battle for the hearts and minds of his fellow Victorian naturalists. When *The Origin of Species* appeared in print on November 24, 1859, Darwin resigned himself to his inability to change the minds of "experienced naturalists" concerning the mutability of species, especially when those naturalists held long-standing views contrary to his own. For those unconvinced Victorian naturalists, species were as immutable as the continents were fixed in place. Darwin knew the doubters would quickly fall back on expressions such as the "plan of creation" and "unity of design," and that they would elevate unexplained and marginal difficulties in his novel mechanism of natural selection to support their predictable rejection of his theory. For Darwin, species were mobile in time and space, just as he was mobile on his salutary circuits around the Sand Walk.

Darwin's hope for vindication of his radical new idea rested with what he called "young and rising naturalists" who had open minds about the transmutation of species and who could impartially look at both sides of the evolution argument before reaching conclusions. The eight young naturalists from the California Academy of Sciences of the 1905–1906 expedition were just what Darwin had in mind. They were not going on a collecting expedition to just any group of volcanic islands. They were headed for classic ground: the Galápagos Islands. Darwin himself had collected there in 1835 and the islands would eventually become inseparable from Darwin as a person and from his newly-published evolutionary ideas of 1859. The islands would become known, in large part due to the huge collections of the 1905–06 expedition, as Darwin's living outdoor laboratory of evolution. The eight young men of the Academy expedition played a pivotal role in cementing

[7] Attributed to Joseph Stalin, September 1943; likely referring to military equipment (tanks), number of divisions of soldiers, or farm equipment.

[8] Web page: *http://www.calacademy.org/geninfo/mission.html#history*. Viewed July 25, 2003.

the name of Darwin to the Galápagos Islands, and the specimens they collected would be the intellectual glue. The islands would become Darwin's islands, just as biological evolution would become Darwin's great intellectual innovation.

The young Academy collectors were open-minded and not firmly committed to either side in the natural selection debate of the early 20th century. Their open-mindedness was tempered by the pragmatic concern of collecting specimens that would be worked up after the expedition by some of those same experienced naturalists that Darwin had worried about as he dipped his pen in the inkwell and as he strolled the Sand Walk. The split commitment to evolutionary theory and specimen collecting by the Academy collectors was due partly to their youth and inexperience: they were not researchers who concerned themselves with matters of theory in the 47 years since the *Origin* was published. Another reason for their lack of commitment was their status in the academic and museum hierarchy: they were not in positions of power or decision-making. They were not the testers of theories; they were the collectors of data. On this Galápagos expedition they mainly sought information on species occurrences on particular islands and in particular habitats. More importantly, they sought the crucial specimens themselves that populated the classic ground of Darwin's islands. As committed to thorough field collecting and as committed to supporting the larger research program of the Academy back in San Francisco as they were, they were led on the expedition by a remarkable man who only had a seventh grade education. Rollo Beck was known as the preeminent collector of his day, and he would remain so for the next 25 years. He was not concerned with supporting or rejecting what Darwin had fretted about at Down House. But the work done by Beck and his capable group of young naturalists would vindicate Darwin many times over.

Down to the Sea in Ships

Loomis put the expedition doctrine right to work. The first of the Academy's larger expeditions involving a sailing vessel to international waters was their 1903 expedition on the schooner *Mary Sachs*[9] to a group of offshore Mexican islands known as the Revillagigedos.[10] Here, under the heat of the tropical sun, the Academy would stake its academic claim to studying and collecting on remote Pacific islands, and Rollo Beck would hone his skills as an expedition leader (Fig. 2). This was the first international collaboration between Loomis as scientist turned consummate museum administrator and Beck as eminent field collector. The Loomis-Beck collaboration was successful and productive.[11]

Loomis wanted to continue his personal research in ornithology "so far as he could find time to do so" and realized that Rollo Beck "would be a valuable aid in that work." Beck and his men

[9] The schooner Mary Sachs was built in 1898 in Benicia, California, and her dimensions were: 56.5 feet long, beam 18.1 feet, draft 5.6 feet, 35 gross tons (31 net tons) and was originally home ported in San Francisco. She was first listed in 1898 with official vessel number 92847 in the "Thirteenth Annual List of Merchant Vessels of the United States" (for the year ended June 30, 1898), Government Printing Office, Washington, D.C., page 131. A glimpse into role of the Mary Sachs in searching for a lost arctic exploration party was garnered from the internet: "No news has been received since April 1914 from Vilhjalmur Steffanson, formerly a student at the North Dakota State University, now with the Canadian arctic exploring expedition last hear of near Herschel Island, according to New York dispatches received here. The dispatch is dated at Shingle Point, MacKenzie Bay. It states that the schooner Mary Sachs, which sailed from Baille Island to Banksland August 19, should be able to advance some distance northward in search for the Steffanson party, as the ocean around Banksland is believed to have been unusually free of ice. The winter base of the schooners Alaska and North Star was established about 15 miles east of Cockburn Point, directly south of Sutton and Liston Islands, the dispatch says. It is added that the prospects are good for the work of the southern party during the next year, as it is well equipped with provisions, sledges and dogs." Source: http://ftp.rootsweb.com/pub/usgenweb/nd/towner/newspapr/ne15fema.txt

[10] Hittell, op. cit., p. 414.

[11] See Dumbacher, J.P. & West, B. 2010 (this volume).

would collect the specimens and Loomis and his colleagues would publish scientific papers. It was a match made in heaven and Loomis took full advantage of keeping one foot in the world of birds and the other in the world of museum administration.

Loomis envisioned the 1903 expedition as a training mission. He utilized the knowledge and skills of the Academy's curatorial staff, while sending out young, and somewhat inexperienced, collectors after first training them in standard collecting techniques and museum preparation techniques. Rollo Beck lead a group of three or four students as his assistants, each paid "one dollar a day and expenses in the field." This was the going rate; equal to what the U.S. Fish Commission paid its field collectors.

FIGURE 2. Photo of *Mary Sachs* docked in San Francisco; photo of collecting crew (from left to right) sitting: E.W. Gifford (conchologist), F.E. Barkelew (botanist), C.H. Marks, Jr. (anthropologist), standing: A.S. Bunnell (ornithologist), J.O. Hultberg (captain), R.H. Beck (chief). (Courtesy California Academy of Sciences Archives.)

Loomis proposed a series of training sessions to prepare the young collectors to bring back high quality specimens. Alice Eastwood would instruct a student in how to collect and preserve plants; John VanDenburgh (1872–1924) and Rollo Beck would each teach a student how to collect reptiles and birds, respectively; and Alfred Kroeber (1876–1960) would instruct a fourth student in collecting anthropological specimens.[12] This method of constituting the 1903 expedition party was mirrored two years later by the 1905–06 Galápagos expedition. Both expeditions relied on relatively young, but reliable, men to collect specimens for a more senior group of curators who stayed back in San Francisco and subsequently published papers on the scientific results of the expedition. This plan worked smoothly with two notable exceptions: At least two multi-year professional conflicts over specimens broke out, involving the botanist and paleontologist from the 1905–06 Galápagos trip.

Loomis hired Rollo Beck, leader of both the Academy's 1903 and 1905–06 expeditions, in January 1903, for $70.00 per month plus his expenses in the field. This was Beck's first steady scientific job, although he had impeccable qualifications stemming from three previous collecting trips

[12] None of the eight young men were trained anthropologists, although E.W. Gifford subsequently became Director of the Lowie Museum of Anthropology (originally located in San Francisco; renamed in 1991 the Phoebe A. Hearst Museum of Anthropology) on the Berkeley campus of the University of California.

to the Galápagos Islands in 1897–98, 1901, and 1901–02. Beck's personal characteristics (he was physically and mentally very tough) and his previous field experience made him well qualified to head an expedition. Loomis placed his faith in Beck to accomplish the lofty expedition goals of the Academy. Beck's formal education did not match his practical education. Growing up in the small town of Berryessa south of San Francisco, Beck did not quite finish the 8th grade and left school at age 12 in 1883, the year after Charles Darwin died. For Beck, shipping out on a series of small schooners would prove to be, as whaling voyages were likewise for Herman Melville's narrator Ishmael, "My Yale College and my Harvard."[13]

The Academy's 1903 expedition to México was a practice run for the larger and longer Galápagos trip. Both trips contained the same basic elements: a group of young men, a small schooner, a group of islands with exotic species, and sufficient time to collect thoroughly. Loomis knew well of the previous collecting trips to the Galápagos financed by individuals such as Walter Rothschild and institutions such as Stanford University. He likewise knew of the fame and prestige brought to anyone possessing specimens from Darwin's Islands. He might not, however, have agreed with Darwin.

A Damnable Shame

Walter Rothschild (1868–1937), the wealthy and eccentric British collector, wrote to herpetologist Albert Günther (1830–1914) in March 1898 expressing these same sentiments. "It was lucky they [a Rothschild financed expedition] went last year; in 3 years time there will not be a living giant Land Tortoise of any kind on the Galápagos Islands, 'What a damnable shame', is it not?"[14] This sad prophecy by Rothschild was a primary motivator for Loomis to organize the 1905–06 expedition.

For the 1905–06 expedition, there was a sense of urgency in their day-to-day activity to collect "fast disappearing species." This amounted to salvage collecting at a time when conservation thinking had not yet become an integral part of every field biologist's code of ethics. Some 26 years after the expedition, the now-middle-aged Joseph Slevin (who was 25 when the expedition set out) wrote about that sense of urgency that pushed the expedition forward.[15] Loomis organized the expedition primarily to make an exhaustive survey of the status of the gigantic land tortoises and to "secure specimens of the various species before it *proved to be too late*." [emphasis added.] For one species of tortoise it was in fact too late, but the agent of extinction was possibly the expedition itself, rather than a nebulous external threat. The subspecies known scientifically as *Geochelone nigra phantastica* Van Denburgh, 1907, is known from a single specimen, collected by Rollo Beck on April 3, 1906. It bears both the museum number CAS 8101 and the distinction of being the only specimen of this subspecies known from the islands.

Ironically, the extensive collecting of the 1905-06 expedition demonstrated that in some ways their concerns, and those of writers extending back to the 1890s, were unfounded. Their extensive collection of 266 tortoise specimens and their survey of every island in the archipelago established that the tortoises were "still living on all the islands in the archipelago from which they were formally known and that they even existed on islands they were never known to be on."[16] Contrary to

[13] Melville, H. 1851. Moby Dick, Oxford University Press (Edition 2008). Last sentence of Chapter 24, "For a whale-ship was my Yale College and my Harvard."

[14] Letter from Walter Rothschild to Albert Günther, dated March 14, 1898, from Günther Correspondence, General Library Maunscripts, L MSS Guunther Collection, Section 19, Box 1 and 2, Natural History Museum, London. [hand-copied by Michele Wellck, October 2002]

[15] Slevin, J. R. 1931, Log of the Schooner "Academy" On a Voyage of Scientific Research to the Galápagos Islands 1905-1906. *Occasional Papers of the California Academy of Sciences* XVII, p. 5.

[16] Ibid, p. 5

their fear of imminent extinction, the tortoises were doing relatively well, even thriving on some islands where they were reported as extirpated.

The same logic and rationale that Loomis applied to the 1905–06 Galápagos expedition had been applied to the 1903 expedition that the Academy "fathered and sent out" to the offshore Mexican islands. By the earliest years of the 20th century, the Academy had made a decision to send out a series of expeditions to "unexplored islands in the Pacific." Following their collecting trip to the Mexican islands, the Academy was originally planning to send additional collecting expeditions to Tiburon Island in the Gulf of California, and then to a series of islands off the coast of Chile. These latter two expeditions never materialized. Instead, the Academy mounted their expedition to the Galápagos.

Destruction of Academy correspondence and records in the 1906 earthquake and fire leaves as a primary source contemporary newspaper articles that describe these expeditions. The 1903 Mexican islands expedition sought "to secure to science some of the valuable and fast-disappearing specimen[s] of animal and plant life from the practically unexplored islands in the Pacific."[17] A motivation for this first international schooner-based expedition, to be echoed by the 1905–06 expedition, was that "Island life all over the world is fast disappearing." The wording in these San Francisco newspaper articles that appeared just before and just after the Academy's expeditions are likely a direct reflection of Loomis' scientific views and his ambition as Museum Director.

When it came to Academy business, Loomis in his capacity as Director controlled the ebb and flow of money, specimens and information. The museum was Loomis's empire. He must have been, using today's terminology, a "micro-manager" when it came to controlling people and events at the Academy's building on Market Street and also when they were far a field collecting. Nothing was done on a daily basis without his written or verbal approval. Larger items were brought before the Board of Trustees for approval, but Loomis dominated the daily hum of activity within the museum walls. Nothing of substance was done without approval from "Mr. Loomis," as they respectfully called him.

For example, Loomis forbade his expedition members from speaking to the press. Each man signed a contract which stated in part: "At no time during the expedition or after your return to San Francisco, are you to covey to newspapers directly or indirectly any information concerning the expedition."[18] Thus, newspaper accounts of the various Academy expeditions are likely the result of typed press releases and/or personal interviews that San Francisco reporters conducted with Loomis.

The agents of biological extinction identified by the San Francisco newspaper stories were feral animals (dogs, cats, rats) brought to remote islands on ships, and partially human activities. In the case of Galápagos tortoises, their bodies were rendered for oil, or consumed outright them for food. After these feral animals dramatically increased in number, they would, the article maintains, turn to eating the native plants and animals. "The result has been," the *Chronicle* stated in August 1903, "that priceless specimens of birds have been destroyed wholesale. The world of science has awakened to the state of affairs, and strenuous efforts are being made in various parts of the world to secure specimens *before it is too late*" (emphasis added). Loomis and his field collectors were on a mission inspired by a desire to short circuit oblivion. They would also visit the Galápagos before it was too late.

The notion that 'time was running' out motivated Loomis and the men on the Galápagos expedition. From their perspective, either they collected as many of the encountered specimens as pos-

[17] *San Francisco Chronicle*, Friday, August 14, 1903.

[18] Contract signed by Joseph S. Hunter and Leverett Mills Loomis (as Agent and Attorney in Fact) on June 15, 1905. CAS Archives, Hunter Collection. Each of the eight young men signed an identical contract.

sible, or it would be "a damnable shame" that species went extinct before they could be documented for science. Better dead and preserved in a museum than left to the whims of feral animals and reckless humans.

Besides the pressing need to collect specimens before what appeared to be imminent extinction, the Revillagigedo Islands, located 300 to 600 miles off the Pacific coast of Mexico, were remote and dangerous to visit. "Several of the young men nearly lost their lives in attempting to make a landing" on the rock-bound coast of Clarion Island. This was one of the expedition's "most thrilling experiences" in these islands "over which the surf constantly breaks."[19] Who could be bothered to return to such remote and dangerous places? Better to collect as much as possible before returning to the safety of San Francisco. The eight young men collected diligently and tirelessly for Loomis so far from home. But conservation and preservation and restoration, as we think of them so commonly today, were not yet on the minds of these young men, or on the radar screen of the general public. That societal transition was actually spurred by an event that took place in Washington, DC, during the expedition: the signing of the American Antiquities Act of 1906, which led, in subsequent years to the growth of the American conservation movement.[20]

The 1903 trip provides a sterling example of how conservation was *terra incognita* for collectors of this era and generation. On San Benito Island in the Revillagigedo group the young men secured, with great difficulty, a specimen of the San Benito or McGregor's House Finch.[21] The significance of collecting this specimen was abundantly clear to the men. "There are only four or five birds of the kind left on the island," the *Chronicle* reported in August 1903, "and they will probably be extinct by the time another expedition visits the place." The Academy visited again in 1925, and the species was last reported alive in 1938. It is now extinct.[22] Speeding species to extinction was not the intention of these collectors, either on the Mexican islands or in the Galápagos Islands. Catching these rare birds was not easy, either. The San Benito House Finch did not give up its feathers easily. "The bird brought back was chased all over the island and finally shot."[23]

After the 1903 expedition, the Academy next planned to visit Tiburon Island in the Gulf of California in February 1904. Here they would be able to acquire "the richest of specimens" on an island inhabited by people "nearest to the aboriginal type of any that have lived in the United States." Despite tales that these people were "cannibals, bloodthirsty and savage," the proposed expedition would collect natural history specimens and "these Indians and their lore will be closely studied." This expedition did not materialize and was superceded by plans for the 1905–06 Galápagos expedition.

Exactly a month before departing San Francisco, on May 28, 1905, anyone reading page seven of the Sunday edition of the San Francisco *Chronicle* would have known in great detail the "whys and wherefores" of the Galápagos expedition. A headline in the well-illustrated article by Edward Berwick proclaimed:

"*Expedition Which Goes After Wonderful Specimens, Fast Becoming Extinct on Galapagos Islands, Is the Most Important Ever Sent Out From the Pacific Coast.*"

Again, as the newspaper had stated just after the 1903 Mexican islands expedition, the emphasis in 1905–06 was on an expedition that sought specimens that were fast becoming extinct, rather

[19] *San Francisco Chronicle*, Friday, August 14, 1903

[20] Webpage: *http://www.nps.gov/history/local-law/anti1906.htm*. Viewed April 15, 2010

[21] Also known also by its Latin name, *Carpodacus mexicanus mcgregori* Anthony, 1897). Fide web page: *http://scilib.ucsd.edu/sio/indexes/campanaz.html* viewed on November 1, 2002.

[22] King, W. Endangered Birds of the World; The ICBP Bird Red Data Book QL676.7.K56 1981, ISBN 0-87474-584-5 Preamble 8; Fuller, E. 1987, Extinct Birds, Facts on File Publications, 256 pp. (p. 188).

[23] *San Francisco Chronicle*, Friday, August 14, 1903.

than specimens in support of a more cerebral enterprise, such as gathering support for Darwin's hypothesis of natural selection. The failure to address theoretical issues reveals the Academy's preoccupation with the more pedestrian topic of specimen-based taxonomic studies.

Remarkably, even 100 years since the expedition set out, it is still the longest and most extensive expedition ever sent to the Galápagos. Berwick's prescience that particular Sunday morning reflected Loomis' grand ambition. After reading about it in the *Chronicle*, San Franciscans knew their museum was setting off to grab the brass ring in the evolutionary Mecca of Darwin's Islands. Even today, the Academy's curators have a firm grasp on the importance of the world's largest collection of Galápagos specimens. As an indication of how important large museum collections are today, 150th anniversary annual report of the Academy in 2003 was titled, "18 Million Real Things."

Setting Sail for Galápagos

After recovering from a collision with the steamer *Argo* at their anchorage on San Francisco waterfront, the crew had the *Academy* repaired and ready to leave San Francisco on the morning of June 28, 1905. Anticipation must have been high among the eight young men and three crewmembers who were about to embark on what they already knew would be a significant voyage. As Loomis explained to newspaper reporters who interviewed him prior to departure, this voyage to the islands would be longer and their collecting would be more detailed than any previous expedition. Clearly, this scientific voyage would bring the California Academy of Sciences fame and treasure, in the scientific sense.

FIGURE 3. 1905-06 Galápagos expedition members: (from left) Frederick T. Nelson (1877–1959), Alban Stewart (1870–1950), Ernest Samuel King (1866-1948), Rollo Howard Beck (1870–1950), Joseph Slayton Hunter (1879–1972), sitting J.J. Parker (navigator), Joseph Richard Slevin (1881–1957), Edward Winslow Gifford (1887–1959), Washington Henry Ochsner (1882–1927), Francis Xavier Williams (1882–1967). Not shown, James White (cook). (Courtesy California Academy of Sciences Archives.)

The big eastern museums had already been to the Galápagos , and David Starr Jordan of nearby Stanford University was a friendly rival of the Academy's Director, Leverett Mills Loomis.[24] This type of rivalry can be very productive, as scientists and institutions leap frog over each other to acquire more numerous and better specimens from increasingly exotic locales.

For now, Loomis's work was done. He had acquired expedition funding, purchased and outfitted a suitable schooner, and assembled a competent field party. There was nothing left for Loomis to do but stand on the dock and wave goodbye.

Bringing the Galápagos Back to San Francisco

By the time Charles Darwin died on April 19, 1882, he had done more for the fame and modern reputation of the Galápagos Islands than a thousand advertising agencies or tourist bureaus. He had, in fact, made this obscure volcanic archipelago, with its odd assortment of plants and animals, the centerpiece of one of the most revolutionary ideas in the history of human thought: biological evolution by means natural selection.

Darwin made the Galápagos Islands more than just a museum of evolution — more than a mere *showcase* of evolution, as they are often described today. He made them the *proof* of evolution. Galileo's believers would rely on images in telescopes and sketches of stars and planets in the heavens. Einstein's believers would rely on complex mathematical and computational proofs on sheets of paper or computer screens. But Darwin's believers would rely on finches and tortoises and iguanas that you could walk among and touch with your bare hands. In the Galápagos, you could reach out and touch evolution.

All of this fame is because Darwin featured the Galápagos Islands prominently in two of his best-known books. The islands got their own chapter, wedged between South America and Tahiti, in his 1839 travelogue of his five-year circumnavigation on the British hydrographic surveying ship HMS *Beagle*, a book that is often simply called *The Voyage of the Beagle*. In the *Voyage*, Darwin described what he saw on the four islands he visited and speculated obliquely about several evolutionary topics. The islands and organisms also appeared prominently in his most famous book, his 1859 landmark work called *On the Origin of Species*. This book contains Darwin's actual mechanism of biological evolution, natural selection, and features several Galápagos examples and references.

These two books, along with Darwin's extensive personal correspondence following the *Beagle* voyage and specialized work done by zoologists and botanists on the animals and plants he collected in the Galápagos formed the core of information that has fascinated biologists ever since. The Galápagos and Darwin are forever linked.

Today, some 170 years after Darwin's visit in 1835, the Galápagos Islands are widely known as Darwin's living outdoor laboratory of evolution. In 2004, a record 100,000 people visited the Galápagos on ecotourism vacations, many of them drawn to the islands made famous by the published work, and well-deserved reputation, of Charles Darwin. Travelers today want to see what Darwin saw, they want to experience what Darwin experienced, they want to see the volcanic birthplace of a revolutionary and tumultuous idea. By and large they are not disappointed.

In addition to the cachet and charisma of Charles Darwin, those advertising agencies and tourist bureaus also got another dream come true — almost all the spectacular wildlife of the Galápagos is perfectly tame and doesn't move an inch, even if you approach to within a few inches.

[24] Larson, E.J. 2001, *Evolution's Workshop: God and Science on the Galapagos Islands*. Basic Books, New York. p. 123.

This place was custom made for tourism. Walt Disney could not have done better if he had tried. But the islands and organisms, and all the drama of predators and prey, volcanoes and ocean currents, blistering tropical sun and torrential El Niño rains, are real, not fake. This is not Frontierland or Tomorrowland or Adventureland. This is where animals and plants live and die, for real, in a harsh, unforgiving environment. This is the crucible of new species.

Catching Evolution in Action

As remote and obscure as the Galápagos Islands were, and remain, Darwin permanently gave these islands the three dream criteria of every aspiring real estate agent: location, location, location. Because of the intellectual connection to Darwin, the person described as responsible for 'giving biologists something to do,' the islands have become the dream vacation spot of every biologist in the world. Ecologically-minded tourists from around the world visit these famous islands, but not as they would one of the Hawaiian Islands at an all-inclusive mega-resort with golf courses, tennis courts, swimming pools, and world-class restaurants. Visitors to the Galápagos visit as Darwin himself did, from a small ship with a slow-paced, island-hopping itinerary. Almost every visitor to the Galápagos recreates the voyage of the *Beagle*, whether they know it or not.

But the technical problem is this: just like the followers of Galileo and Einstein, the followers of Darwin are seeking something elusive, intangible, and largely invisible. Today's Darwinians are seeking to observe a *biological process*, which takes years and years to play out. The drama they are drawn to might occur high in a tree, deep down in a burrow, far out to sea, or even under water. So most visitors to the islands must make due, when they visit for a week or 10 days, with seeing the *products* of evolution by natural selection — the finches, and mockingbirds, and cacti, and tortoises, and iguanas, and flightless birds that populate the small cluster of islands. Even the most careful observers can rarely catch evolution or natural selection in action. Most of us have to settle for the results, the box scores, if you will, after the game has finished and winners and losers can be clearly identified.

The same dilemma of viewing the *products* of evolution rather than the *process* of evolution, existed 100 years ago when the California Academy of Sciences decided to visit the Galápagos Islands in 1905 and 1906. They traveled as Darwin did by visiting in a sailing vessel, but they surpassed Darwin in several important ways. The Academy's objective was clear and well prescribed: collect the *products* of evolution and bring them back to San Francisco for study and publication. Their plan was simple, and at the same time grandiose: send a group of eight young sailor-scientists down to the Galápagos to collect for an entire year — Darwin had only been there for five weeks[25] — and return with a bounty of specimens. The goal of the expedition was to *collect evolution*.

The vigorous intellectual debate that followed publication of *The Origin of Species* only strengthened the allure of the Galápagos. One could *read* the book and vicariously partake in the controversy, or one could *go visit* the Galápagos and participate in the controversy first hand.

In the early summer of 1905, the curators at the California Academy of Sciences decided to both read and visit: they sent the young collectors to the Galápagos while they themselves stayed home in San Francisco, with the ultimate goal of publishing papers on the results of the expedition. Today, the curators would make up the core of the expedition, and young, inexperienced collectors would come along only as subordinates. Indeed, in a modern professional *volte-face*, scientists today are expected to participate in field expeditions, whether to collect dinosaurs in Mongolia or

[25] Grant, K.T. & Estes, G.B. 2009. *Darwin in Galápagos: Footsteps to a New World*. Princeton University Press, 348 pp.; Keynes, R.D. 1979. *The* Beagle *Record: Selections from the original pictorial records and written accounts of H.M.S.* Beagle. Cambridge University Press, Cambridge. xiv + 409 pp.

to collect ants in Madagascar. In fact curators today would actually lose scientific respect among their peers if they simply stayed back at the museum and did nothing more than publish papers based on specimens others had collected. But 1905 was a different time, and a major expedition to the Galápagos would take well over a year. The senior staff could not spare that time.

Scientific conceptions of the islands have not stayed constant since Darwin's visit in 1835. The extent to which scientific perceptions of the islands have changed emerges from the details of the chapter in Galápagos science written in history by the eight young men on the schooner *Academy* in 1905 and 1906 — but a chapter whose story has only been sketched in print. This is also a chapter in the growing legitimacy of science in the American West in the late 19th and early 20th centuries, and the seminal role of the California Academy of Sciences in that growth.

Summary of the Expedition

The 1905–1906 expedition lasted 17 months. The eight young men spent a year and a day in the islands, the longest duration single scientific expedition in Galápagos history. The California Academy of Sciences expedition visited all of the 13 major islands (several times in some cases), and most of the smaller islets in the archipelago. In comparison, Charles Darwin was in the islands for five weeks and visited just four islands. The Academy expedition collected some 75,000 biological specimens — more than any Galápagos expedition before or since. The collectors brought back over 260 preserved specimens of giant tortoises, as well as numerous other reptiles, birds, mammals, insects, plants, land snails, and fossils. The enduring legacy of this expedition is the collections made by the intrepid "eight young men" who severed as sailor-scientists aboard the schooner *Academy*. In effect, they brought the Galápagos back to San Francisco.

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Collecting Galápagos and the Pacific: How Rollo Howard Beck Shaped Our Understanding of Evolution

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Rollo Howard Beck, born in Northern California in 1870, became one of the most productive and accomplished ornithological collectors of all time. With less than an eighth-grade education, he learned to prepare scientific museum specimens of birds and eggs, learned the most modern photographic techniques, and became an accomplished sailor and expedition leader. He traveled along the western seaboard of both North and South America and throughout the islands of the South Pacific. His most important expeditions include the Webster-Harris Expedition and the California Academy of Sciences' Expedition to the Galápagos Islands, the Brewster-Sanford Expedition to South America and the Caribbean, and the Whitney South Sea Expedition. The birds he collected have become the basis for several important works, including David Lack's classic book on Darwin's finches, and Ernst Mayr's work on evolution in South Pacific birds. We focus here on his work as a young biologist in the Galápagos; however, we summarize his greater contributions to Ornithology and the importance of his life's work.

KEYWORDS: Ornithology, Galápagos, birds, collecting, Rollo Beck

Biologists often risk their lives to explore new places, document natural history, and amass the collections that provide a foundation for biological knowledge. Natural history collections offer the most tangible, complete, and permanent record of biodiversity on earth. These collections are the basis upon which species are named, species ranges are mapped and known, and variation within and among species can be studied. Other sources of information (field guides for example) gather species identification information primarily from natural history collections.

The collectors themselves have amazing stories to tell. In order to amass the collections found in today's natural history museums, individuals took great personal risk and years away from home. Creating these collections takes skill and care, oftentimes amidst drama and adventure.

Foremost among bird collectors stands Rollo Howard Beck. Beck is unrivaled in having produced large series of beautifully prepared birds from the Galápagos Islands, and these have contributed greatly to our understanding of evolution. Beck is also recognized for having been the world's pre-eminent seabird collector and one of the most productive ornithological field researchers and collectors of all time. Beck collected in the continental US, Mexico, Alaska, South America, Australia, and numerous Pacific and Caribbean Islands. Beck was innovative for being the first to chum for seabirds and designing a special toothed spoon for stripping fat from birds. He was an accomplished natural history photographer in the early days of photography, an amateur anthropologist, and an excellent sailor and expedition leader.

In 2009 we celebrated the bicentennial of Charles Darwin's birth and the contribution that Darwin and the Galápagos have made to our understanding of evolution. The Galápagos has been an excellent laboratory for studying evolution, in part because of the interesting biology and geology of the region, but also because of the massive natural history collections available for study. Although he first visited the Galápagos 62 years after Darwin, Rollo Beck, perhaps more than any other single person, has contributed to building Galápagos natural history collections.

This paper records the professional life and major expeditionary work of Rollo Beck, mentions some of the scientific impacts that his specimens and other work have had on biological thinking, and finally addresses some of the controversies that his work has created.

Beck's Early Collecting

Beck was born in Los Gatos, California on 26 August 1870, and grew up among the apricot and prune orchards of the Santa Clara valley (Beck 1936). There he spent a great deal of time outdoors and trapped gophers before and after school. He learned to identify birds, prepare skins, and mount specimens from his neighbor, Frank H. Holmes, who had trained with the ornithologist Theodore Sherman Palmer. In 1885, at age 14, Beck prepared the first of many birds, a Common Nighthawk (*Chordeiles minor hesperis*) that was sent to the Smithsonian. Although Beck left school before completing the eighth grade, he continued to study ornithology with his friends and joined the American Ornithologists' Union in 1894. He corresponded with many of the top ornithologists of the day, including Robert Ridgway and Captain Charles Bendire, whom the still–young Beck remembered for offering encouragement in exchange for information on birds and eggs of lesser-known California species. In 1894 Beck also joined the newly formed Cooper Ornithological Club, based in San Jose, California. Beck was an active member, and regularly went on collecting trips with fellow club members including Wilfred H. Osgood. On various occasions with Osgood, Holmes and others, Beck collected in the Sierra around Lake Tahoe and the Yosemite Valley, and in 1896 collected the first eggs and nests of the Hermit Warbler and Western Evening Grosbeak, of which he was very proud.

In June 1895, the 24-year old Beck traveled south to Santa Barbara and out to the Channel Islands, collecting. Again in the spring of 1897, he hitched up his horse to his spring wagon and drove 300 miles to Santa Barbara, this time to collect for the California Academy of Sciences. He made friends with a schooner captain, Sam Burtis, with whom he sailed among the northern Channel Islands of Santa Cruz, Santa Rosa, and San Miguel. He collected multiple specimens and records of birds while there, but Beck was most proud of his early records and descriptions of Island Jay eggs and nests, which he believed to be the first ever collected. With these specimens and reports of new findings, his reputation spread eastward. The experience of sailing and visiting these near-shore islands helped prepare him for an upcoming opportunity to join the Webster-Harris Expedition to the Galápagos Islands.

The First Trip to the Galápagos

The Webster-Harris Expedition was funded by Lionel Walter Rothschild, from Tring, England. Rothschild was the son of the wealthy European banking family and a lover of natural history. On his 21st birthday his family gave him money to erect a sizeable natural history museum in the English countryside. He sponsored many collectors and expeditions to bring him animals from around the world, with a special fondness for birds, butterflies, and giant tortoises. He leased Aldabra Atoll (part of the Seychelle Islands in the Indian Ocean) for many years in order to protect the endemic giant tortoises living there. In 1897 Rothschild contracted Mr. Frank Blake Webster of Hyde Park,

Massachusetts, to organize a large collecting expedition to the Galápagos Islands. Webster, who didn't accompany the expedition, hired Charles Miller Harris as the first taxidermist. The other men on board included Captain Samuel Robinson, Otis Bullock, James M. Cornell, and George Nelson. The party set sail from New York on 29 March 1897 aboard the Steamer *Valencia* bound for Panama, where they planned to secure a sailing vessel and launch the expedition to the Galápagos (Rothschild 1983). Once in Panama, they found it impossible to charter a seaworthy boat at a reasonable price. Other troubles plagued the team. Bullock turned out to be an unmanageable alcoholic and was subsequently sent home. Yellow fever felled Captain Robinson, who died in Panama and required an alarming proportion of their funds for doctors' fees and funeral arrangements. The three remaining team members decided to sail for San Francisco and look for a boat there, but Cornell and Harris both came down with yellow fever during the voyage. Cornell died on board, and Nelson deserted immediately after arriving in San Francisco (Rothschild 1983).

Harris, the taxidermist, recovered from his fever and took over the leadership of the expedition in San Francisco. With money from Rothschild and Webster, the 150-ton 95-foot two-masted schooner *Lila & Mattie* was chartered with captain and crew. Webster hired two new East Coast taxidermists, Galen D. Hull and Frederick Peabody Drowne, and was seeking an additional collector when the name of Rollo Beck was suggested (Rothschild 1899).

Unaware of the expedition, Rollo Beck had already left with his cousin for a field trip to the mountains. Just as they crested the Sierra near Lake Tahoe and passed the last stage station, they stopped to see if any mail had been sent for them. There was a telegram from Frank Blake Webster asking if Beck would join an expedition to the Galápagos. Beck immediately sent a telegram in return, answering "Yes," and turned his horse around to head back to the city. Beck was hired for $25 per month without commission or rank. To save costs, Webster arranged for the collectors to arrive in San Francisco as close as possible to the departure date; they would sleep aboard the *Lila & Mattie* until departure. The trip was on.

Rothschild's instructions set the tone for the most systematic and complete collecting style. The expedition was to first visit the unexplored islands, as unknown species would be most likely to lurk in such places. As for creating the series of specimens, Rothschild continued, "you will carefully go over the entire ground of each island securing birds at least 50 of each kind." (Larson 2001:117). Until well after Darwin's *Origin of Species* was published, it had not been the practice to collect large series of a single species. After the acceptance of Darwin's views on species, large series became important to describe the variation within a species as well as between species. Rothschild's request reflected this change in focus, which Beck was more than happy to accommodate. These large numbers and complete series were especially demanded in the Galápagos, as Rothschild continued, "the slightest difference in bill or size while the bird in other respects be the same they would be different." (Larson 2001:117). As for tortoise, they were to collect every specimen that they could obtain, large or small, dead or alive. Rothschild's parting rally was that, "We look to you to outdo expeditions of Darwin, Baur, Agassiz and others. Believing that I have selected a party with nerve, backbone, and energy, I am yours very truly" (Larson 2001:117). This energy and philosophy of collecting were properly imparted to Beck, and Beck retained this spirit throughout his career.

Beck certainly learned many additional things while on this voyage. He collected seabirds in addition to land birds. Although most of the seabird collecting took place in rookeries rather than at sea, many seabirds are large and require special techniques for capturing and handling. Seabirds also often have significant fat reserves under the skin and often require special techniques for skinning and stuffing. Beck also learned about and practiced photography on the trip, as there were a camera and 144 photographic plates carried onboard. Some of the photos were used later to create

sketches for Drowne's published diaries (Rothschild 1899). Miriam Rothschild reported that the photos were all lost after arriving at Tring (Rothschild 1983); however some photos have survived at the British Museum of Natural History Archives and perhaps one or two others in Beck's personal collection, now in the California Academy of Sciences' Archives.

Beck's knowledge of sailing must have grown tremendously during this long open-ocean voyage. Sailing in the Galápagos is challenging — currents are strong and winds blow and fail fitfully, anchorages are often poor or lacking entirely — and in Harris's estimation the captain was overly careful. The harrowing stories of yellow fever from Harris probably impressed Beck during this trip too, and Harris's own "yellow" fevers came and went while in the Galápagos (which more likely indicates malaria rather than yellow fever). They prudently avoided landing in Panama or other tropical American ports as every other ship landing reported fever-related deaths of passengers, and Beck learned to do the same on future voyages. Lastly, Beck learned of a buried pirate treasure on Genovesa (Tower) Island (Beck 1936). Birds alone were enough to keep Beck collecting, but the rumor of buried treasure appears to have helped keep Beck's focus on the Galápagos. Beck apparently used the lure of buried gold to entice others to join him on future trips to the Galápagos.

Beck impressed Walter Rothschild and others with field skills as well as his drive and stamina. Miriam Rothschild related the difficulties of tortoise collecting with the following story, partially taken from Harris's diaries:

> "By noon, we had just got the tortoises secured and were two miles from lunch and our water was short. Two men each took a tortoise lashed to a pole and started for the coast. It was the hardest work I ever did for my part and I guess that the rest thought the same. At 4 o'clock we got to shore above a high bluff. We tied them here for the night and started for the boat two miles across the island. This was very tough work. No dinner. No water. The sailor Charles was completely exhausted after reaching the boat at dusk." Beck, it seems, was made of sterner stuff, for he then "secured a rat." (Rothschild 1983:199).

Seven and a half months later, the Webster-Harris Expedition returned with 60 crates packed with 3075 bird skins, 400 bird eggs, 150 iguanas, 65 tortoises, 40 tortoise eggs, 13 seals and sea lions, 8 sea turtles, several hundred lizards and other miscellaneous zoological items (Rothschild 1983). One of the great discoveries was the Galápagos Flightless Cormorant (*Phalacrocorax harrisi*), named in honor of Harris. The volume and quality of specimens was impressive given that they had spent only about three and a half months in the Galápagos. When they returned, Harris was waylaid in San Francisco tending to the remaining live tortoises, and Rothschild was immediately soliciting Beck to return for more reptiles.

Back to the Galápagos Again and Again

While seeking a ship for another Galápagos trip, Beck wrote to Ridgway asking if the Smithsonian had any particular wishes for Mexican or Galápagos birds. Ridgway provided lists, and Beck sent him at least 92 skins from the next two trips down the Mexican coast and 86 skins from the Islands. After a failed 1899 attempt to return to the Galápagos (ending in a shipwreck in Magdalena Bay, Mexico), Beck again put together an expedition to Galápagos in November 1900 aboard the schooner *Mary Sachs*. Along the way, Beck collected on Guadalupe Island, and saw 11 Guadalupe Caracaras (*Caracara lutosa* then known as *Polyborus lutosus*). He collected 9 of them and shot at the remaining two that got away (Abbott 1933). Beck was the last person to see this species alive. The team spent two and a half months in the Galápagos before returning to San Francisco with about six dozen tortoises (including a male and female of the rare Pinta tortoise) and an

unknown number of bird skins, which were offered to Rothschild. Beck led another small expedition to the Galápagos in December 1901, via Mexico, Clipperton, and Cocos Island and was in the Galápagos for about four and a half months. Rothschild and Hartert were especially interested in these other islands as well, as the Webster-Harris Expedition had to abandon their plans of collecting on them due to the delays in Panama and expense over-runs. By this time Rothschild no longer wanted everything, and he provided Beck with a list of the things he sought as well as those he did not want, instructions which Beck followed only sometimes. During these years, Beck became more confident and experienced on the ocean and working with teams of collectors. He asserted his own independence as a trip organizer and leader.

On these subsequent trips to Galápagos, Beck also did a great deal of photography and further developed his skills. He published several of his photos in the *Condor* (Beck 1904) along with life history notes. His abilities as a field collector clearly impressed Rothschild, and after this second trip, Rothschild invited Beck to bring the entire consignment in person to London – complete with a live Barn Owl, six land iguanas and about 60 tortoises. The amounts Rothschild paid for the specimens made a lasting impression on Beck (Beck 1936), and were probably instrumental in helping Beck realize that he could make collecting a lucrative profession.

The California Academy of Sciences and the 1905-06 Galápagos Expedition

Back in San Francisco, Beck began working for Leverett Mills Loomis, then the Director of the California Academy of Sciences. Loomis was interested in seabirds in the order Procellariiformes (albatrosses, petrels, and shearwaters), and he hired Beck to collect them from 1903 through 1910. Beck collected mostly around Monterey Bay but also took two longer coastal trips — one to the Santa Barbara Islands and another to the Revillagigedos Islands, off the coast of Mexico, in 1903. By this time, Beck was experimenting with chum to attract seabirds, and later became famous for finding birds at sea that even long-time sailors had never seen (Murphy 1936). His work in Monterey provided many interesting records, including the first West Coast records of Flesh-footed Shearwaters, and documented the presence of Pomarine Jaegers, Sooty Shearwaters year round, and Parakeet Auklets wintering.

Now 34 years old, Beck's next big opportunity came when Loomis conceived of another large collecting trip, this time to the Galápagos. The California Academy purchased the decommissioned schooner *Earnest* from the US Coast Guard, and refitted her for a large ocean collecting trip, renaming her the *Academy*. Loomis was personally interested in seabirds, but as museum director, he sought the most authoritative collections from every taxonomic group. In addition to Beck, the team included two ornithologists (Edward Winslow Gifford and Joseph Hunter, who also worked on mammals), two herpetologists (Joseph Slevin and Ernest King), an entomologist (Francis Xavier Williams), a malacologist and geologist (Washington Henry "Doc" Ochsner), and a botanist (Alban Stewart). Not only was Beck hired as a collector, he was appointed head of the expedition. A navigator was hired to pilot the ship, and although Beck often referred to him as "Captain" in his field notes and log, it was clear that Beck was in charge. Never one to waste money, Loomis had all but Beck sign on as seamen as well as collectors, thus enabling him to save on seamen's salaries.

Loomis planned to out-collect Rothschild, much as Rothschild had out-collected Darwin, Agassiz, Baur and others. Fears had grown, and Beck's photos had documented (Fig. 1), that the wildlife was being decimated by whalers, sailors, and locals at an alarming rate so a race was on to document Galápagos species before they disappeared entirely. Rothschild had predicted that the tortoises would be extinct in less than three years, regardless of scientific collecting and had written to the herpetologist Albert Günther as early as March 1898:

FIGURE 1. Beck took this photo showing the devastation the oil hunters wrought. Probably 1901. (G11, Rollo Beck Collection, California Academy of Sciences Archives.)

> It was lucky they [the Rothschild-financed Galápagos expedition in 1897-98] went last year; in 3 years time there will not be a living giant Land Tortoise of any kind on the Galápagos Islands. What a damnable shame, is it not? (*Letter in collection of the Natural History Museum, London, courtesy of Michele Wellck, CAS Archives*)

Loomis mobilized the press, and there was much fanfare. Celebrations were held on board, the boat was christened, and the newspapers covered the events. Just hours before their departure, the steam schooner *Argo*, coming into harbor collided with the schooner *Academy*, and ruptured three boards above the water line on the schooner's port beam. The damage was sufficient to require cargo to be shifted to starboard to prevent taking on water, and repairs were immediately begun. With the repairs completed in two days, the schooner *Academy* was taken out the Golden Gate by tugboat on 28 June 1905.

The voyage was challenging from the start. Most of the men were immediately seasick, and the main peak block was carried away within hours of being at sea, requiring repair before the mainsail could be used again. Showing his skill as a sailor and documenting one challenge of sailing the schooner, Beck recorded in his journal "Ship [down by] stern, & keel not far enough forward, makes it difficult to sail on wind." (Beck, 6 July 1905, field journal, Rollo Beck Collection, California Academy of Sciences Archives). Throughout the trip, there was often mention of minor repairs that were required to keep the schooner sailing. During the voyage the *Academy* was careened, its bottom scraped and repainted, and sails were removed, repaired and "bent on" (remounted), all impossible without the help of the collector-seamen. The bunks were small and space was tight (Fig. 2), as much of the ship was converted to storage for specimens. It was a con-

FIGURE 2. Beck "off watch" in a bunk typical of early expedition schooners. Beck was only 5'8"; note his bent legs. (G161, Rollo Beck Collection, California Academy of Sciences Archives.)

stant battle to keep the cockroaches and bedbugs under control. Beck wrote "Used cyanide, potassium, 6 oz., & other dope to kill bedbugs, etc. Killed most mosquitoes & cockroaches but no bedbugs." (Beck 14 Jan 1906, field journal).

Beck the Collector and Leader

In Beck's diaries and letters, we gain insight into the type of leader he was. He was fit and tough, and led largely by example. He clearly did not ask anything of the men that he would not do himself, and for the most part he contributed as much labor and at least as many specimens to the endeavor as the others, all the while accomplishing the extra duties required for leadership. He often landed on his own, slept under the stars on the ground (reporting being fed on by ticks and insects), collected and skinned, always helping the others with tortoises. From the journals it appears that the men got along quite well, and this too speaks highly of his leadership abilities. Although the expedition lasted over 17 months and involved grueling work, only a couple of fights were reported, and these were mentioned only in Beck's diaries. About one argument, Beck remarks laconically "no official knowledge" (Beck, 22 January 1906, field journal). After the navigator had given several demonstrations of incompetence, poor judgment, and picking fights with Slevin and Ochsner (at least), the collectors signed a letter asking for either J.J. Parker's resignation or theirs, and delivered it to Beck. Beck handled this too with utmost care and professional formality. Parker was dismissed and later left on Albemarle Island. Afterward Beck assumed complete control of the vessel as well as the rest of the expedition.

The diaries also offer some hint of Beck's personality. Early in the expedition, while crossing

FIGURE 3. This was the *Academy*'s first stop on the way to Galápagos. Note that one person is circling his creel around his head to ward the birds off; the other has hold of a frigate bird by its feet. San Martin Island, Mexico, 1905. (G173, Rollo Beck Collection, California Academy of Sciences Archive.)

the equator, one reads, "Crossed the line. Neptune came aboard but was overpowered & ray necks kept from getting shaved." (Beck, 18 September 1905, field journal). This refers to the sometimes violent tradition of one of the seasoned sailors dressing up as the god Neptune and hazing the new timers. We assume that it was Beck who played Neptune on 18 September 1905, and apparently he was overpowered by the new-timers and collected several bruises and a cut at the edge of his eye.

On one occasion, he with three others found themselves at the shoreline with a small skiff, trying to transport three large tortoises to the schooner *Academy* through heavy seas (Beck, 17 March 1906, field journal; *Slevin Log* [1931]). The skiff overturned, and subsequently was smashed to smithereens, leaving the men a swim to shore and a two-mile walk in the dark over a'a lava, to the place the *Academy* was anchored. Beck had lost his shoes so made this walk barefoot. He says "I had on stockings

FIGURE 4. Hunter and Beck in a frigate bird colony. Note the young frigate in the lower left. 1905. (G174, Rollo Beck Collection, California Academy of Sciences Archive.)

FIGURE 5. Nelson, mate on the *Academy*, contributes a boar to the larder. Cocos Island 1905. (G223, Rollo Beck Collection, California Academy of Sciences Archive.)

... I stepped on cactus leaves & spines several times & cut finger falling on a lava boulder in grass." (Beck, 17 March 1906, field journal.) Slevin, somewhat less stoic and missing only his shirt, said "As we walked through the brush in the dark, I felt as if there was not a cactus or thorn bush on all Albemarle Island that I missed running into. However, I wouldn't have traded places with Beck for anything." (Slevin 1931:92.)

On another occasion, Beck found a small finch "on back on ground, tangled up in some sticky burrs, feebly struggling, a dove or two watching. Evidently feeding & burrs fell on back & stuck. I pulled out a lot from back & wing & neck & bird hopped off. Would pull out himself viciously all he could reach, feathers & all." (Beck, 27 October 1905, field journal). One wonders whether this release was whimsical mercy or a specimen too damaged to be collected.

As trip leader, he was more concerned with food than the others, and so he often mentioned when animals were collected for the larder. These included "doves for breakfast," "cakes with turtle eggs very good" and "tern eggs very good baked or in cakes or scrambled" among many other references. Many of the foods eaten included introduced species, especially pigs and goats (Fig. 5). Beck also mentions horses, burros, wild dogs, and other introduced species that the team encountered. These records now provide excellent information about the distribution of introduced species on the islands during that time. They also illustrate the necessity of finding food to sustain such an expedition, and hence the practice of introducing species such as goats – a practice that Beck employed in the South Pacific and for which he was later criticized. The 1905-06 expedition for the California Academy of Sciences was Beck's fourth trip to the Galápagos. By the end he established himself as the preeminent Galápagos collector, hands down. Not only did he know where to find a particular bird or tortoise, but he also knew where the anchorages were, when it was safe to use one, as well as a good deal about the winds and currents. The success of the expedition also established him as a capable expedition organizer, leader, sailor, and natural historian.

The success of the expedition also re-established the Academy after the great earthquake and fire of 1906:

> The Galápagos Expedition put the Academy 'on its feet' as far as materials for a new museum is concerned. This Expedition left San Francisco on June 28, 1905, returning Thanksgiving Day, 1906, with some 5000 reptiles, 38000 shells, 1000 tertiary invertebrate fossils, about 13000 insects, about 10000 plants, 8688 birds, about 2000 eggs, many nests, and about 120 mammals. (Gifford 1908:95).

The precision in the number of birds reflects Gifford's interests; according to his collecting journal he collected 3409 of the 8688 birds (of which 3072 made it into the CAS collection). Beck contributed about 2100 to the CAS collection, and Joe Hunter contributed another 2200 or so.

The materials from this trip are well preserved. Each collector on board kept a journal, all of which are held in the California Academy of Sciences Archives. They have been transcribed by the generosity of Matt James and colleagues and subsequently edited into publishable form by Barbara West. In addition, Beck and Gifford left a wonderful series of about 350 photographs (plus another 120 photos from Beck's earlier visits). Much has been written about the history of the schooner *Academy* expedition (see James, this volume). In addition, some 20 papers were published in the California Academy of Sciences *Proceedings*, plus five in other journals and about 12 books.

After the Galápagos Expeditions

After the 1905-06 Academy expedition, Beck continued to work for Loomis in Monterey and northern California (Fig. 6) rebuilding the collections that were lost in the 1906 San Francisco earthquake and fire (Beck 1910). By 1907, Loomis began talking about a possible expedition to Hawaii, again with Beck in charge. Beck was interested, but was also working on his personal life. He asked Ida Menzies of Berryessa to be his wife and join him on this — and future expeditions. They were married 9 August 1909. But when Beck asked Loomis for a raise — a reasonable request based upon his experience and past successes working with the California Academy, and probably also having to shoulder the extra responsibility of being married — Loomis denied him the raise, purportedly due to lack of funds. At the age of 40, Beck left the California Academy of Sciences after seven years (1903–1910) of individual and expedition collecting for them.


FIGURE 6. Beck at home in his workshop, shortly after returning from the CAS Galápagos Expedition. (N29755, Rollo Beck Collection, California Academy of Sciences Archive.)

Beck quickly took up with Joseph Grinnell of the University of California's new Museum of Vertebrate Zoology (MVZ) located in Berkeley. Beck conducted two solo expeditions collecting seabirds (Monterey Bay, 1910–11) and water birds (Los Baños, 1911–12) of northern

California. Grinnell was interested especially in the distribution of California birds and how geography and local habitat led to differentiation. Beck's collections were targeted to answer specific questions about species boundaries — both according to geography and niche.

Beck's fame as a collector continued to spread. In 1911 Beck received a letter from Dr. Leonard Sanford of New Haven, offering considerably more money to collect for him. Sanford was a wealthy professor at Yale medical school and a dedicated collector of birds. He was also by then a good friend of Frank M. Chapman, curator of birds at the American Museum of Natural History (AMNH) in New York. Chapman offered Sanford an office space at the American Museum next to his own. Sanford accepted and brought his substantial personal collections and helped fund additional collectors working for the American Museum bird collections, including Rollo Beck. This was a valuable connection, as Sanford's money and connections would facilitate Beck's later work around South America and in the Pacific.

In 1911, under Sanford's and the AMNH's sponsorship Beck accompanied Arthur Cleveland Bent and Alexander Wetmore for a five and a half month collecting trip to the Aleutian Islands and the area around Nome, Alaska. Bent was working on his large series *Life Histories of North American Birds* for the Smithsonian Institution, and he was interested in bird specimens as well as eggs and nests. Alexander Wetmore, who would become famous for his work with the US Biological Survey and the Smithsonian, was along on the trip as well. Beck now had worked with leading ornithologists of the American Museum and the Smithsonian, the two most wealthy and powerful museums in America.

When Beck returned from the Alaska trip and was once again working for Grinnell, Sanford continued to send requests for various specimens, particularly a rare shearwater, and funded a short trip by Beck to Guadalupe Island, Mexico, in August 1912, followed by more collecting around Monterey. In a September 1912 letter Sanford said, "We will probably start you southwards early in October. So make … a special attempt to get the rare shearwaters." In an October 5 letter Sanford says "Regarding Mrs. Beck suit your own convenience. I appreciate perfectly your position and would want under similar circumstances to do the same. I thought it would be more comfortable [if she followed later]. But do as you please. I am hoping to hear that you picked up the two rare shearwaters." We don't know if Beck got the shearwaters that Sanford so badly wanted, but we do know that Beck made preparations to bring his wife, Ida, on his next big adventure.

Brewster-Sanford Expedition — South America and The Caribbean

On 4 December 1912 Rollo and Ida Beck departed by steamer to South America. Dr. Sanford had proposed a two-year trip along the South American coast. It was extended to nearly five years, included collecting in the Andes and in much of the Caribbean, and was ultimately funded by another wealthy AMNH benefactor, Frederick F. Brewster. The Becks alternated between commercial vessels and chartering smaller boats to take them where there was no commercial traffic.

They spent the next eight months in Peru, about two-thirds of the time along the coast, the rest of the time in the Andes, hiking up to 16,000 feet. It was when Beck was in Peru that Murphy (1936) later told the famous story about Beck's prowess as a collector:

> When Mr. Rollo H. Beck, a veteran student of marine birds, was collecting for The American Museum of Natural History in Peru, he chartered a coasting sloop under command of an experienced native skipper and sailed several days' journey off shore. The subsequent enlightenment of the Peruvian sailors was related to me by my friend of the Chinchas, Captain Charles Niehorster, who was a member of the crew.

> One quiet morning early in the course of the voyage, Beck remarked that he would like to lower a boat for birds.
>
> 'But there are no birds here, señor,' said the skipper, waving an arm around the circle of blank water.
>
> Nevertheless, a skiff was sent down, and Captain Charlie manned the oars. For two miles or more he pulled straight ahead, while Beck methodically tossed flecks of oil and grease and scraps of meat in the boat's track. Then they doubled on their course, and to Charlie's amazement the long food-line was soon dotted with unfamiliar, dainty sea-sprites, which skipped and danced like butterflies along a blossoming hedge-row. A series of many birds, including specimens of Hornby's Petrel, was brought back to the sloop, and displayed before the doubting crew.
>
> 'But we have never before had such birds as these in Peru, señor,' insisted the Captain. And his men unanimously agreed. (Murphy:1936:8).

Almost another year, August 1913–July 1914, was spent continuing down the coast of Chile with a side trip to the Juan Fernandez ("Robinson Crusoe") Islands, arriving in Punta Arenas, Chile, in Tierra del Fuego, in the dead of the austral winter (Figs. 7–8). A month was spent collecting locally, then they headed north on a steamer from Punta Arenas and spent three months collecting around Mar del Plata, Argentina, "waiting for the summer to begin at Cape Horn."

In early November 1914 they headed south again, spending the next six months around Tierra del Fuego. Although storms would last for days at a time, Beck would collect on whatever island he could get to. On 22 December 1914 they rounded False Cape Horn, on the 29th the true Cape Horn, thus fulfilling a dream of Beck's. But he was never one to say "Enough!" so they sailed another 10 miles south before the weather turned on them, and they fled back to the closest shelter. They continued to move from anchorage to anchorage as the weather allowed, and Beck collected both on land and on the water. On 1 September 1915, near Rio Gallegos, Beck laconically recorded "in chasing a couple of wounded geese through a pond had to

FIGURE 7. This shows the Beck's route around South America and through the Caribbean. Brewster-Sanford Expedition, 1912–1917. See Fig. 8 for details of Tierra del Fuego routes. (Route map compiled by J. Woram).

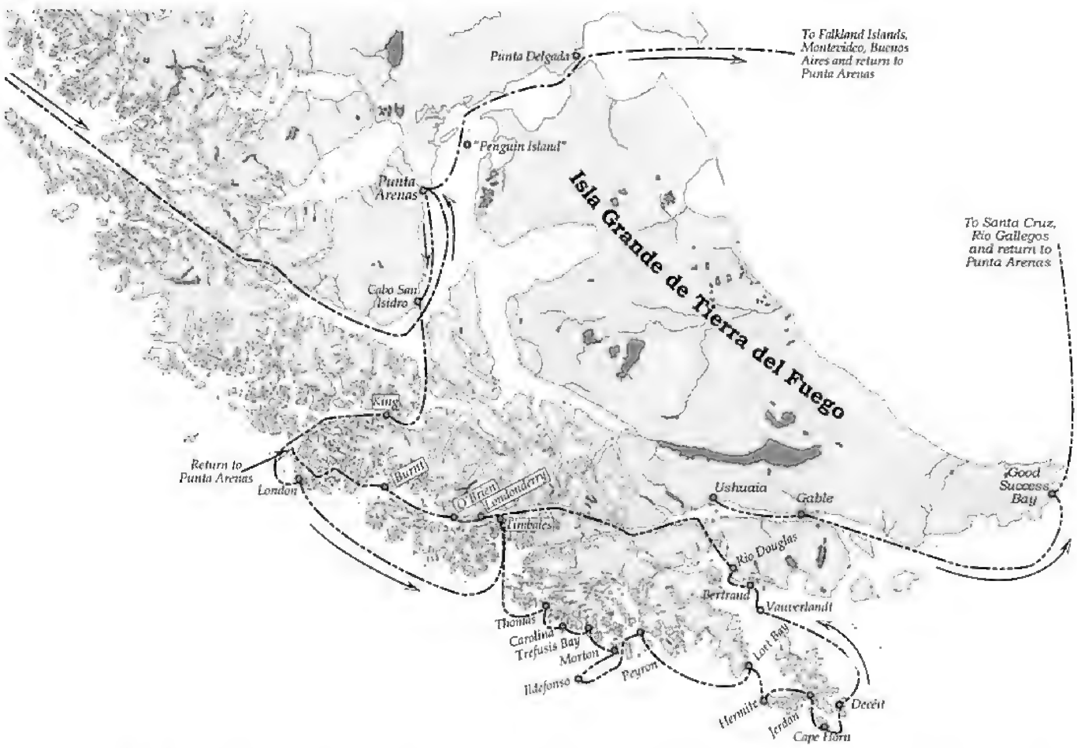

FIGURE 8. The Becks crossed back and forth through the Tierra del Fuego, spending eight and a half months in this region, twice fleeing back to Rio Gallegos, Argentina, to escape the worst of the austral winters. July 1914–October 1915. (Route map compiled by J. Woram; base map courtesy of S. Zagier).

break the ice with my bare feet." After about 10 months around Tierra del Fuego, on 11 October 1915 they returned to Punta Arenas, their headquarters for this period. The next stop was the Falklands where they spent three months collecting (Fig. 9).

FIGURE 9. The Becks in the Falklands with a few thousand of their closest rockhopper friends while on the Brewster-Sanford Expediton. November 1915–January 1916. (Courtesy of the Library, American Museum of Natural History).

Finally, in February 1917, they turned north for the last time. They spent several months along the coasts of Argentina and Brazil waiting for collecting permits that never came. Then from August 1916 to August 1917 they collected in the Caribbean, including St. Thomas, Dominica, Santo Domingo, Haiti and Cuba. A wire from AMNH bid them return to New York City where they arrived in early September, thus ending four and three-quarter years of collecting.

In 1919, Dr. Sanford, for AMNH, asked Beck to return alone to Alaska, to collect along the

North Pacific coast. He started in Kodiak on 12 August, passed through Seward and Juneau, and finished in Sitka on 8 October. The letter asking him to make this Alaska trip dangled another temptation before him. "I am particularly anxious to have you return from [Alaska] in season to get a good rest for a possible South Sea Island expedition within a year." (Rollo Beck correspondence, California Academy of Sciences Archives).

Whitney South Sea Expedition

The "possible South Sea Islands expedition" became the Whitney South Sea Expedition (WSSE), sponsored by AMNH and funded by Harry Payne "Jock" Whitney. Whitney was a businessman, horse racer and member of the prominent and wealthy Whitney family of New England. He was a friend of Sanford and Chapman, and Sanford effectively persuaded Whitney to give over $100,000 for the South Sea Expedition, which paid for the first five years. Like the Brewster-Sanford South America Expedition, the Whitney South Sea Expedition was supposed to last two years. It became a 9-year voyage for the Becks and a 20-year overall effort for AMNH. Ida and Rollo took a commercial vessel to Tahiti, arriving 25 September 1920. The intent was to use cargo and fishing vessels to get around the South Pacific islands but, as was true for the South American expedition, the result was a great deal of time lost, waiting for a boat going the right place. By 1921 Beck had convinced AMNH that it would be better to purchase a sailboat with an engine. It took nearly a year but finally a vessel was found which fit both the requirements and the budget. The log of the *France* started 1 February 1922, as the Becks with two other collectors left Papeete to explore other parts of the Society Islands.

By July 1923, the Becks had spent three much enjoyed Bastille Days in Papeete and Beck had collected French Polynesia to his satisfaction (Fig. 10). The first three assistant collectors had left and been replaced by three others. The Cook Islands and Samoa occupied another 10 months, Fiji and adjacent islands (Fig. 11) another 12 months. By June 1926 the *France* reached Tonga with

FIGURE 10. This roughly shows the Beck's route through the South Pacific. They arrived in Tahiti on a commercial steamer and worked west from there. Whitney South Sea Expedition 1920–1928. (Compiled by Dept. Anthropology, California Academy of Sciences for a web exhibit on Rollo and Ida Beck).

Beck and one other collector, José Correia with his wife, where they spent two months. After a relaxing collecting stop in New Zealand, Beck and the *France* went to the Australian Great Barrier Reef where the Correias rejoined him in January 1926. They subsequently backtracked to the islands off the east and south of New Zealand during February and March 1926 and then proceeded to the Vanuatu archipelago. In mid-December the Correias left the expedition, and in mid-June 1927. F.P. Drowne, who had been one of Beck's fellow collectors on the 1897-98 Rothschild trip to the Galápagos, joined the expedition. By the end of the month they were in the Solomon Islands group, where they remained until the end of December 1927. Two additional collectors, Guy Richards and Hannibal Hamlin joined the *France* in mid-October. In January-February 1928, Drowne, Richards, and Hamlin collected on Bougainville Island while Beck collected alone in the Bismarck Archipelago. In mid-February 1928, the Becks left the *France* in the command of Hamlin, and taking the log book, they started for Sydney, Australia, from which they expected to return to California.

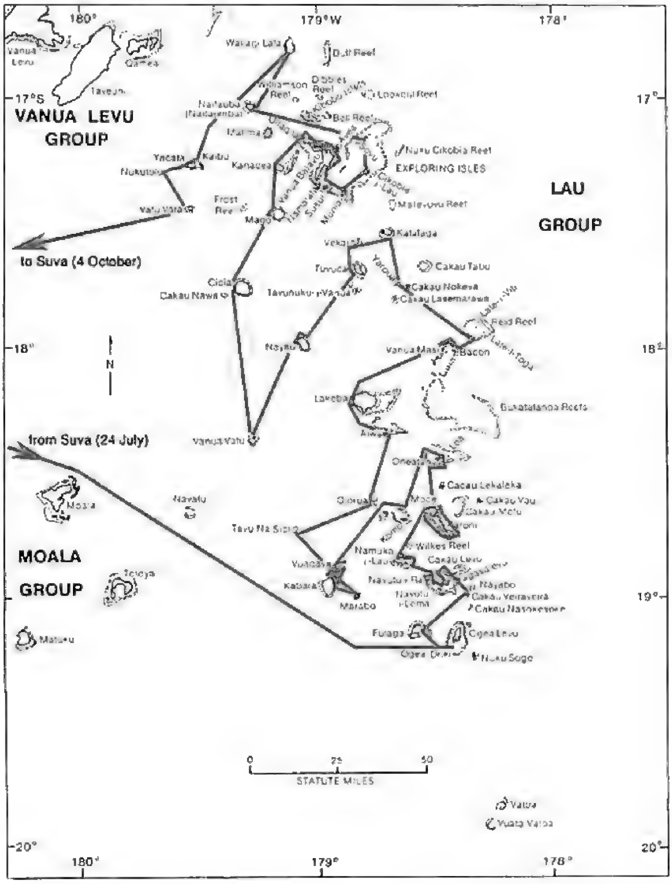

FIGURE 11. Their actual route was much more complicated. This is the detail of the route of the *France* through the Lau island group, 1924. (Map from Evenhuis 2007, map 2 [courtesy Bishop Museum]).

However, a telegram caught up with the Becks while at sea on the way to Australia. George F. Baker, a trustee of the AMNH offered to support them, separately from the Whitney South Sea Expedition, on a collecting expedition to the large island of New Guinea. Beck agreed, and after he and Ida spent a couple of months in Sydney they returned to New Guinea, arriving on 5 August 1928 and staying until 29 April 1929. Beck concentrated his collecting inland on the north coast of Papua New Guinea around Madang (Figs. 12–14). In his collecting journal, Beck reports one of the aggravations of collecting: "continued to collect about Madang, getting 6 species had not taken before but hotel cat climbs up in wardrobe and picks two small specimens from top shelf, leaving only the hind legs of each with label attached" (December 12–27, 1928). He also updated his observations about malaria: "heavy continuous . . . doses malaria kept me near skinning table this week so I conclude quinine is steadily needed" (April 18, 1929). Today AMNH lists 1741 skins collected by Beck on this New Guinea Expedition.

As was his practice, Beck asked the locals to bring birds to him and he purchased those of interest. "Gorgeous birds are blacktailed [*Astrapia rothschildi*, a bird of paradise] as collar in front

glows like golden fire with purplish sheen … breast and lower part deep green with brown band reddish gold about lower throat and the neck of long extremely soft black feathers, these reaching nearly to tip of bill…. I have been hunting two or four times a week for five weeks where these birds occur without seeing one of these adult males." (March 24, 1929). Although this bird (Fig. 16) was apparently new to Beck it was not new to the world, having been described and named in 1906.

While in the South Pacific, Beck wrote about his travels and experiences there for *Natural History Magazine*, the popular magazine of the American Museum. In one of Beck's last WSSE articles published, he recalls discovering Baker's Bowerbird in the mountains above Madang town, Papua New Guinea (Beck 1929).

FIGURE 12. Ida Beck looking at birds brought by a local woman. (Negative no. 115711 [photo by Rollo Beck], courtesy of the Library, American Museum of Natural History).

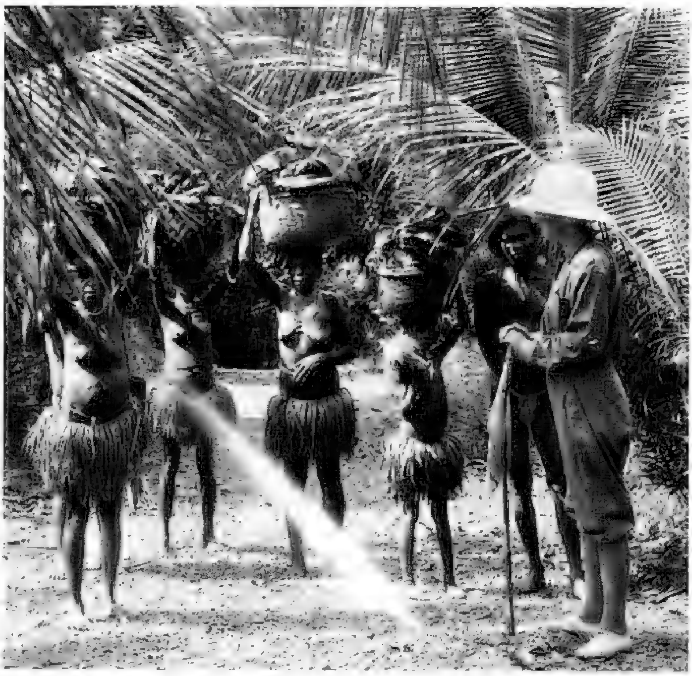

FIGURE 13. This was taken in the Solomons. On the right, Ida Beck in jodhpurs and pith helmet, talks with four local young women. The man standing next to her is probably her guide. (Negative no. 115367 [photo by Rollo Beck], courtesy of the Library, American Museum of Natural History).

After his world travels

On their way home from Papua New Guinea and the South Pacific, the Becks returned to Australia, and then set out for California via Lahore, where Rollo's sister was an M.D., married to a Methodist missionary. From there, they traveled to Egypt, England, Ontario province, where Ida was born, New York City, Washington D.C., and finally back to their farm in Planada, California by early 1930. Here they settled down for the next 20 years. Members of his family have said that in the early to mid-1930s Rollo was diagnosed with cancer, perhaps of the throat or neck. He

FIGURE 14. Ever the helpmeet as well as fellow collector and preparator, Ida seems to be bringing lunch for Rollo and herself. Papua New Guinea. (Rollo Beck Collection, California Academy of Scienecces Archives, with permission from American Museum of Natural History).

FIGURE 15. The *France* at anchor, Vella Lavella Islands, Solomons group. (Negative no. 115392 [photo by Rollo Beck], courtesy of the Library, American Museum of Natural History).

was treated with radiation, apparently successfully, because this did not appear to have any bearing on his later health.

During these years Rollo continued to observe and collect birds. He reported primarily to the state Fish and Game Commission, which now required permits to collect, and he offered his specimens to the local museums. His energy focused on variation in species and subspecies of local birds, including especially red-winged blackbirds (all vermin in his view) and the perplexing variation in dowitchers. Although having no formal training in ornithology, let alone taxonomy, Beck kept up with the literature and followed up when he saw something that didn't match his collecting experience. In 1932, William Rowan published an analysis of dowitcher taxonomy, separating the long-billed (*Limnodromus scolopaceus*) and short-billed species (*L. griseus*), and named a new inland subspecies (*L. g. hendersoni*) (Rowan 1932). There was much disagreement among ornithologists about the California representatives — for example, Robert Orr of the California Academy of Sciences and Joseph Grinnell of UC Berkeley Museum of Vertebrate Zoology lumped these all into a single species, and synonomized *L. g. griseus* and *L. g. hendersoni* (Orr 1940; Grinnell and Miller 1944). Beck collected "a couple dozen," and later "a few hundred" dowitchers and presented them to Grinnell, asking him to reconsider Rowan's suggestion. Grinnell and Robert Orr both looked at the problem over the next several years but Beck was not assuaged and kept collecting (as long as the California Division of Fish and Game would give him a collecting permit) and observing. In 1946, Beck was still pushing the issue.

What Beck had observed and others had not, was that the short-billed species occurred mostly in a salt-water environment while the long-billed species occurred primarily in freshwater environments. In 1950, Frank Pitelka published a definitive monograph (Pitelka 1950). Pitelka inspected over 2900 *Limnodromus* held in various North American collections and concluded that Rowan

was mostly right, but that Beck's observations provided key insights into the ecology and taxonomy of the dowitchers. In the monograph, Pitelka gave an amazing tribute to a man who hadn't finished eighth grade, saying "This study owes its origin to the perspicacity and efforts of the veteran bird collector Rollo H. Beck of Planada, California." (Pitelka 1986:387). Later genetic analyses have supported the observations of Beck and Pitelka, showing that the Long-billed and Short-billed Dowitchers are clearly distinct species (Avise and Zink 1988).

During the 1930s and 1940s Beck had a box of fresh fruits from his farm delivered each year to Grinnell and later Alden Miller and the staff of the UC Berkeley Museum of Vertebrate Zoology, and often to the California Academy of Sciences as well. All recipients were delighted both by the thoughtfulness and by the deliciousness of the apricots and figs.

In November 1950, Rollo Beck died at the age of 80, having been active as a farmer and collector until the late spring of that year. Ida remained on the Planada farm for several years, then went to live with a niece and her family until her death in 1970.

Ida Menzies Beck

Rollo Beck's wife and companion, Ida Menzies Beck, was of Scottish descent and born in Ontario, Canada. She moved to California when she was young, and we are not sure how Ida and Rollo met, possibly as childhood friends or possibly through the Methodist Church, to which they both belonged. Ida was good-natured, quick to laugh, and she adored Rollo. Ida and Rollo were married in 1909 by a relative of Rollo's, and they never got the Hawaiian honeymoon that they had hoped for. After being separated for a long time when Rollo worked with A.C. Bent in Alaska, Ida and Rollo decided that they would never again be apart for so long, and that Ida and Rollo would travel together on all of their future expeditions. Together they climbed to the high Andes and Lake Titicaca, and they sailed throughout the Pacific to New Guinea. By all accounts, Ida was tough as nails. She suffered terribly from sea sickness, and like Darwin, she never really got over it, yet this

FIGURE 16. Ellis Rowan, Rothschild's Bird-of-Paradise, or Rothschild's *Astrapia* (*Astrapia rothschildi*), Papua New Guinea, 1917 (nla.pic-an6633368 PIC R1949 LOC 6561, National Library of Australia).

did not prevent her from traveling. Photos typically show Ida in nice dresses and shoes not typical of field attire. Unfortunately, relatively little is written about her role on the expeditions, but it is clear that she assisted in a variety of ways, including those typical of a female companion from that era. She also helped with collecting, prepared specimens, and she knew her birds well. It also appears that her presence helped make peaceful connections in many of the remote outposts and villages that they visited, and that she probably kept the *France* and various field camps up to a livable standard. In their early years in California when Rollo would take a small skiff out into Monterrey Bay alone, she would often wait for him onshore, well after dark, to ensure that he made it back safely. Rollo and Ida had no children, and Ida lived for another 20 years after Rollo's death. During her later years living with Rollo's niece, Ida often regaled the family with tales from their travels and work abroad.

Collectors, Then and Now

To appreciate better what Beck accomplished in his lifetime, we ask what it takes to be a successful natural history collector. Obviously the requirements have changed over the centuries, but what did it take a century ago, when Beck was a master of the art?

Foremost, field collectors needed to know significant natural history in order to spot rapidly a different flight pattern, an aberration in color, size, or geographical range, and immediately recognize its importance. Collectors were also skilled hunters and were required to collect a series of each slightly different bird species. They needed an aesthetic sense, so that each specimen could be beautifully and uniformly skinned and stuffed so that shapes and colors were clearly visible and reflected the appearance of the live bird. The specimens needed to document precisely those characters that caught the collector's interest, including notes about its behavior and ecology.

FIGURE 17. Beck referred to this as Baker's Bower Bird (*Xanthomelus bakeri*), although it is more commonly known as Adelbert Bowerbird; adult and young males. Rollo Beck discovered this bird in the Adelbert mountains in northern New Guinea. Beck 1929. (Reprinted from Natural History Magazine, 1929; Image # 5838 American Museum of Natural History Library, with permission.)

Especially in Beck's time, to work successfully in field conditions the collector needed robust

physical health and stamina. Physical health required several things, including a cast–iron digestive system for any traveler. The collector needed to withstand sea-sickness, drink local water sources, and stomach *E. coli* and other standard infections. When carrying or finding food and water in the field, they had to tolerate a variety of sources, some of which were questionable. Other diseases such as malaria, yellow fever, or dengue could compromise an expedition or one's life. Clearly some degree of tolerance was genetic, but collectors like Beck survived by constant vigilance, by continually making wise and healthy choices.

A degree of mental health and stamina was also necessary for the collector. Beck needed to tolerate difficult conditions, including the extremes of working alone a long way from help, or alternatively, piled atop one another for several months in a cramped ship. He needed to have patience, tolerance, flexibility, and be able to maintain his focus on his work despite the many hardships and challenges.

In addition, Beck needed the skills of expedition leadership. Planning and logistics of large, remote expeditions were overwhelming. Gathering food, supplies, medical equipment, and balancing personalities all required considerable organization and skill. Difficult judgment calls were endlessly required. Keeping the staff healthy, happy, and working hard was challenging, and Beck clearly led his collectors with his own hard work.

Today, many facets of field collecting have changed. Collectors often enjoy many modern comforts and better medicines in the field. Tools such as field guides, recorders, cameras, computers, and internet all make biological information more accessible and easier to collect. Ethical expectations have also changed considerably. Collectors today are held to very different standards, largely because of our knowledge that collecting can adversely affect natural populations. Thus, collecting must be done cautiously using all that we know about the existing populations and their breeding cycles while doing our best to reduce population impact. This largely means reducing the number of specimens collected, and making use of "salvage" – that is, animals that have already died (road kill, window strikes, oil spills, wildlife hospitals, etc.). With fewer specimens, there is increased pressure for more data or material per specimen, including more measurements, notes on soft part colors and on behavior, skins with full or partial skeletons, tissues, stomachs and contents, etc. The esteemed ornithologist Elliot Coues suggested that "fifty birds shot, their skins preserved, and observations recorded is a *very* good day's work." [italics original] (Coues 1903). Today an experienced skinner and collector might only expect to prepare (with notes, tag, and associated materials) one bird per hour (Winker 2000) as compared with one every ten to fifteen minutes in Beck's time.

Navigating complex permit and record-keeping requirements is another facet of modern collecting that was much less burdensome in Beck's age. Today, depending upon where one collects and where specimens finally reside, permission is required from multiple authorities, including permission from landowners or land managers, US Fish and Wildlife Service, state and local departments of fish and game, US Department of Agriculture, and Center for Disease Control, plus any overseas permits for collecting, using firearms or mist-nets, Convention for International Trade in Endangered Species (CITES), import-export documents, and even some perpetual responsibilities are owed to foreign permit bodies. Typically materials are shipped or carried as luggage in planes, so additional laws regulate hazardous materials, packing and shipping requirements, biosafety and potential pathogen issues. Many would-be collectors are discouraged by these complex, poorly documented, and ever-changing bureaucratic requirements. Even many already-dead salvage birds are discarded because of the permit uncertainties or the lack of time or expertise to comply with all of the various agencies. In part for these reasons, our generation's record of the modern biodiversity is lacking in comparison to that of a century ago.

The Impact of Rollo Beck on Ornithology

Beck had a tremendous impact on ornithology, primarily through his collections. The sheer number of his collections is very impressive. At the time of this writing, it has become relatively easy to search museum catalogs online and to compile the numbers from the major collections. Table 1 tallies Beck's specimens from several of those major collections. Both the Smithsonian and the American Museum, due to their massive collections, are still digitizing their data, and so some specimens are likely missing from the tallies. AMNH has graciously estimated the collections attributable to Rollo Beck based upon summary accession cards and concluded that approximately 44,000 of their specimens are attributed to Beck.

To put these numbers into perspective, other major collectors have made the history books for adding 10,000 to 40,000 specimens to various museums (Mearns and Mearns 1998). Today, most ornithologists do relatively little collecting, and even those who do find it difficult to achieve the speed at which Beck was able to skin (Winker 2000). Beck was legendary for being able to cut open, skin out, close and finish a songbird skin in approximately five minutes.

But it is not only the numbers in his collections that make them important, but the way in which they were collected. He was guided in his collecting efforts chiefly by questions about natural variation, species limits, evolution and biogeography. Those he collected for, including Rothschild, Loomis, Grinnell, Chapman, and Murphy, each made clear the scientific questions driving the collections, and Beck made sure that the material was sufficient to answer the questions.

Beck's collections and their impact on our understanding of Galápagos finch evolution.— The history of Galápagos finch taxonomy is an excellent example of Rollo Beck's impact on ornithology. Before Beck's first trip to the Galápagos with the Webster–Harris expedition, ornithologists were unsure how many finch species inhabited the islands or how they were distributed among the islands, although it was becoming clear that this was key to understanding their origin and history, and perhaps evolution in general. Charles Darwin had only collected 65 bird specimens in the Galápagos (Steinheimer 2004), and these were worked up and formally described primarily by John Gould (Gould and Darwin 1839). It was Gould, not Darwin, who first realized that the small dark passerines belonged to a single group of finches. Darwin noted "the most curious fact is the perfect gradation in the size of the beaks in the different species of Geospiza, from one as large as that of a hawfinch to that of a chaffinch, and (if Mr. Gould is right in including his sub-group, Certhidea, in the main group), even to that of a warbler" (Darwin 1845:379). Darwin furthermore suspected "that certain members of the series are confined to different islands; therefore, if the collection had been made on any one island, it would not have presented so perfect a gradation" (Darwin 1839:475). Darwin also wrote, "*Geospiza*, *Camarhynchus*, and *Cactornis* belong to one type, but with regard to *Certhidea*, although Mr. Gould confidently believes it should also be referred to the same division…he would by no means insist upon the above view being adopted, until the matter shall have been more fully investigated." (Darwin 1941:105.)

The next significant collections of Darwin's finches were made by Habel in 1868 and reported by Sclater and Salvin (Salvin 1876). Salvin disagreed with Gould and believed that the genera *Camarhynchus* (tree finches), *Geospiza*, (ground finches), and *Certhidea* (warbler finches) differed significantly and represented three lineages (*Geospiza*, *Camarhynchus*, and *Certhidea*) that independently invaded the Galápagos (Salvin 1876).

The productive Smithsonian curator Robert Ridgway also had an interest in Galápagos birds, and published a large monograph in 1896 based upon the expeditions of the *Albatross* and collections made by Baur and Adams in 1891. Despite having larger collections, Ridgway noted that, "Not a single island of the group can be said to have been exhaustively explored, and few of the

species are known in all their various phases; in fact, many are known only from a few specimens in female or immature dress." (Ridgway 1896:459). The sampling was still better than what was previously available, but "owing to the gradual transition from one form to another, and the almost perfect resemblance between them in coloration, I have found it impossible to construct an analytical 'key' to the species after the usual plan." (Ridgway 1896:509). Ridgway goes on to construct a taxonomy with genus and species names, but it is clear that he considers these to occur along a continuum, and that hard stops do not truly exist in the islands. By Ridgway's reckoning, there were 36 species of finch, plus another 8 species of *Certhidea*, thereby recognizing 44 species of what we would consider today as 13 Galápagos finch species.

In 1899, Lionel Walter Rothschild published a monograph on the Galápagos avifauna (Rothschild 1899) and focused a great deal of attention on the finches. His work was based largely on the collections produced by Baur and Adams in 1891, which he had purchased, but these were now augmented by the Webster-Harris Expedition that Beck participated in and Rothschild privately funded. He proudly concluded that "This material is perhaps larger than any material ever brought together from any area of similarly small dimensions,"(Rothschild 1899:136) and argued that it can indeed begin to reveal the evolutionary history of the islands and speciation in general. Yet, he only draws a single major conclusion — that the entire island's fauna is derived from the Americas. (His second "conclusion" was that it is uncertain whether there has ever been a land connection among the islands or between the islands and continental America.)

Rothschild's taxonomy disagrees in various aspects with Ridgway's. To examine the classic examples, Ridgway recognized eight mockingbird species in the Galápagos; Rothschild recognized eleven. With the exception of *Certhidea*, Rothschild groups all of the finches into the single genus, *Geospiza*, and comments extensively on Ridgway's unjustified splitting of the genera and some species. Rothschild recognized 33 taxa in the genus *Geospiza* and another nine taxa in the genus *Certhidea*. Like Salvin, he did not recognize that *Geospiza* and *Certhidea* were close relatives.

Rothschild also determined that the Cocos Island Finch (*Pinaroloxias inornata*) was actually a thin-billed relative of *Geospiza* (Rothschild 1903). This proved to be a critical link in helping later associate the Warbler Finch, *Certhidea*, with *Geospiza*. (Rothschild additionally reported on a nice age series of Galápagos boobies that allowed Rothschild and Grant to determine that one that had been formerly described as the adult of the *Sula variegata* was actually a new taxon, the Nazca Booby [*Sula granti*] and Beck was "warmly congratulated.")

After the California Academy of Sciences' 1905–06 expedition led by Beck, sufficient numbers of specimens were now available to provide definitive taxonomic resolution and answers to several evolutionary questions. Based upon these specimens, a half dozen important monographs were published, including Gifford's field notes on the land birds of Galápagos and Cocos (Gifford 1919), Loomis's monograph of the Procellariiformes (Loomis 1918), and Swarth's monograph of Galápagos avifauna (Swarth 1931). Some of the impacts included Gifford's copious notes on avian behavior, including the first published observations of tool use in the Woodpecker Finch (*Camarhynchus pallidus*), Swarth's creation of the Galápagos finch family, Geospizidae (Swarth 1929), and a relatively definitive taxonomy for Galápagos birds and phylogeny for the finches (Swarth 1931). Swarth published a version of a finch phylogenetic tree as seen from the roots looking up into the branches, and with obvious lack of resolution at the base but he clearly delineated the different groups and recognized the close relationships between the Warbler Finch (*Certhidea*), the Cocos Island Finch (*Pinaroloxias*), and the other geospizid finches (Fig. 18). For the most part, he understood the relationships among species and depicted them well in that figure. Swarth estimated 35 taxa, all of which he considered species, but he grouped them together much as we do now. Today, we recognize 13 valid species of Geospizidae living in the Galápagos. With sub-

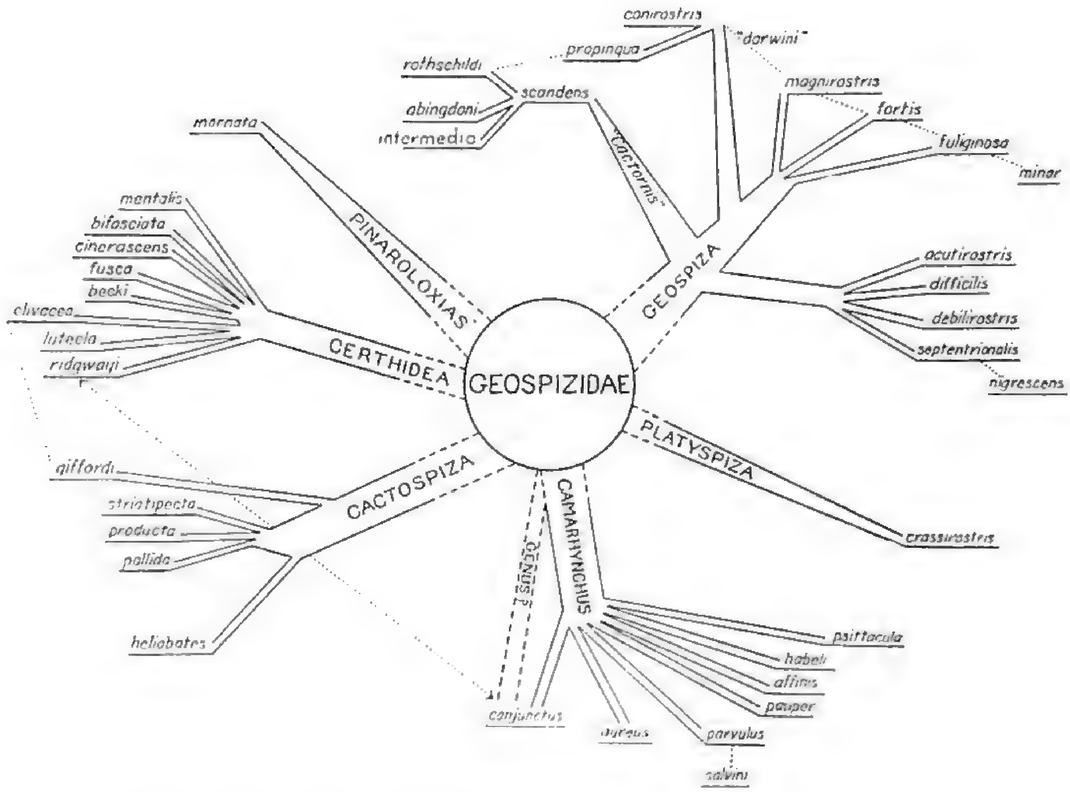

FIGURE 18. Whyte's drawing of the Geospizidae evolutionary tree. (Swarth 1931:139, fig. 19).

species, there are a total of 32 recognized unique taxa. An additional genus and species, the Cocos Island Finch (*Pinaroloxias inornata*) makes the final, 14th species in the avian family Geospizidae (Dickinson 2003). When Swarth's 1931 monograph was written, Swarth had not yet been to the Galápagos, so his work was based solely on specimens from Beck's and others' trips to the those islands.

The next person to make exceptional use of Beck's Galápagos finch specimens was David Lack. Lack traveled the Galápagos from 14 Dec 1938–3 April 1939, and studied the behavior and life histories of the Galápagos Finches. He made copious field observations that are written up in two major published works (Lack 1945, 1947). From the Galápagos he came to the USA and performed thorough examinations of morphology in the collections, especially those of the California Academy of Sciences, Rothschild's collections as well as others at the American Museum, Smithsonian Institution's National Museum, Stanford University (Hopkins-Stanford Expedition (12/1/1898-6/10/1899) and others. Lack's monograph of 1945 has become a classic work in numerical taxonomy, and his second monograph (Lack 1947), a classic work in evolutionary ecology.

There is a fascinating story to be told here, because although the data are basically the same in both of Lack's volumes, the conclusions vary considerably. Lack (1945) quotes Darwin (Darwin 1888):

> But how is it that many of the immigrants have been differently modified, though only in a small degree, in islands situated within sight of each other, having the same geological nature, the same height, climate, etc? This long appeared to me a great difficulty: but it arises in chief part from the deeply-seated error of considering the physical conditions of

> a country as the most important; whereas it cannot be disputed that the nature of the other species with which each has to compete, is at least as important, and generally a far more important element of success. (Lack 1945:117.)

But afterwards Lack (1945:117) goes on to say, "There is no evidence of Darwin's suggestion. In fact, there is no evidence whatever, in any of the island forms of Geospizinae, that their differences have adaptive significance." Lack is satisfied that isolation and genetic drift are sufficient to explain how differences might arise, and considers less how such differences might persist. He presents a beautiful series of figures (Lack 1945, figs. 5–26) presenting morphological measurements of various species occurring in sympatry, uses the differences among the populations and the gaps between them to diagnose the species, and he discusses the ratios of measurement among species and their ecological significance. His conclusions are that three major circumstances shaped the evolution of the finches: 1) the almost complete absence of food competitors, 2) the almost complete absence of predators, and 3) opportunity for temporary isolation of different island forms (Lack 1940).

After several years to think about and discuss the data with friends, Lack (1961:Preface) reverses course and concludes that selection has indeed played a fundamental role. The same data from these same collections of finches are used, and Lack's figure (1947, fig. 17) sums up beautifully how the presence of one species has led to shifts in the mean measurements of sympatric species (see Fig. 19). Lack became convinced that bill size was related to food taken and that differences in bills reflected differences in foraging niches. With Galápagos finches as the example, he showed that 1) interspecific competition is a powerful force that structures communities of species, and 2) ecological isolation is as important as reproductive isolation for species to co-exist. Lack used these two ideas and his data on finches from various islands to construct a model of how finches likely radiated into many species. Lack's 1947 book, *Darwin's Finches: An Essay on the General Biological Theory of Evolution*, has become a classic volume in evolutionary ecology for its insights into interspecific competition, natural selection, and speciation. The later work of Robert Bowman from San Francisco State University has further demonstrated the adaptive values of beak differences (Bowman 1961) and the tremendous life-long work of Peter and Rosemary Grant and their students have shown how this natural selection works in wild Darwin's finch populations (Grant 1986; Grant and Grant 2007 and this volume).

The impact of Beck and the WSSE on Ernst Mayr and the New Evolutionary Synthesis.— The Whitney South Sea Expedition helped launch the career of the renowned evolutionary biologist and ornithologist, Ernst Mayr. In 1927, Mayr was an assistant at the Berlin Museum working with Erwin Stresemann. Stresemann recommended Mayr to Ernst Hartert (Lord Rothschild's curator of vertebrates) and to Leonard Sanford at AMNH for a joint collecting trip to New Guinea. Mayr was sent to collect birds in Dutch New Guinea (now Papua, Indonesia) from April 1928. He then crossed the border to Mandated Territory of New Guinea (now the northern half of Papua New Guinea) in December 1928, where he collected for another five months. While Mayr was in the field for Stresemann, Robert Cushman Murphy of the AMNH solicited Mayr to assume leadership of the Whitney South Sea Expedition after Beck's retirement. Being in the field so far from communications, Mayr received and then complied with the invitation too late. By the time he arrived at Samarai Island, Milne Bay Province, Papua New Guinea, to lead the expedition, William Coultas had already assumed leadership at Murphy's request. Mayr still joined the expedition in July 1929, and traveled on the *France* for eight months through New Guinea and the Solomon Islands, eventually returning to the Berlin Museum in February 1930 (LeCroy 2005).

Due to mounting pressure on the AMNH to demonstrate tangible results from the WSSE, Mur-

phy again hired Mayr for one year beginning in 1931 as a visiting Research Associate in the Department of Ornithology at AMNH to work up the material collected during the WSSE. During this year, Mayr published six papers from the South Pacific specimens. In 1932, Lord Rothschild sold his bird collection to the AMNH, and Mayr was permanently hired as curator of birds and tasked with the enormous job of unpacking and cataloging the Rothschild collection as well as curating the continually growing WSSE collection (Rothschild 1983; LeCroy 2005). With the combined collections of Rothschild and the AMNH, Mayr had access to an incredibly expansive and thorough bird collection from the southwestern Pacific, and probably the most complete from any part of the world.

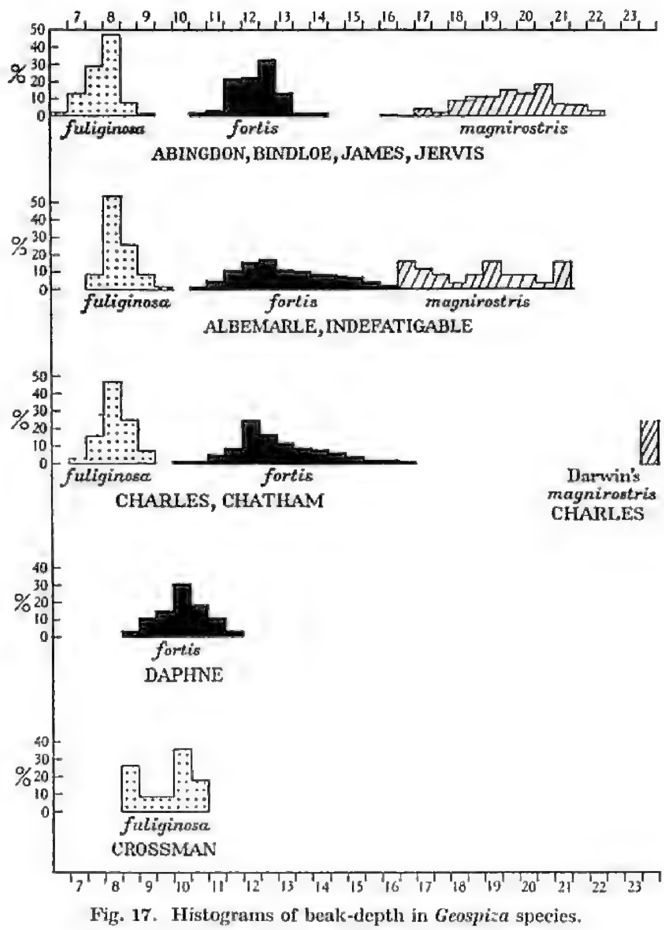

FIGURE 19. Lack's careful measuring of beak-depth in *Geospiza* produced these figures showing how different Galápagos islands had variants of beak-depth in the same species (Lack 1947:82). (Reproduced with permission from David Lack's Estate).

In the coming years, Mayr published 41 papers based upon the WSSE materials, only four of which were coauthored (LeCroy 2005). Mayr also published the definitive monograph on the birds of the southwest Pacific (Mayr 1945) and the checklist of the birds of New Guinea (Mayr 1941). These empirical studies provided the foundation for Mayr's understanding of geographic variation and speciation, especially his ideas concerning the role of allopatry in speciation. These ideas were later compiled in his classic book, *Systematics and the Origin of Species* (Mayr 1942). This volume is now a classic in evolutionary biology and was an integral element of the "modern evolutionary synthesis" that melded Darwinian evolution with early 20th century understanding of genetics (Larson 2004). Incidentally, Lack wrote his first monograph on Galápagos finches in 1939, published in 1945 (Lack 1945) and then a second monograph (Lack 1947). Mayr's 1942 book certainly was read by Lack between his two monographs. Other major contributors to the synthesis offered mathematical theories of genetics (Sewall Wright and R.A. Fisher) and laboratory studies of evolution (Theodosius Dobzhansky), but Mayr contributed a deep understanding and numerous examples of evolution in natural populations, inspired largely by his work on South Pacific birds (Schodde 2005).

Although they both collected in New Guinea at the same time and both were deeply involved with the WSSE, Beck mentions Mayr only three times in his log, only one of which indicates that

Beck and Mayr actually met on the Huon Peninsula. At that time neither had any reason to think that Mayr would be invited to join the Whitney Expedition (personal communication from M. LeCroy). Nonetheless, Beck's collections and the work of the WSSE significantly influenced Mayr. It was also the strong start of the WSSE that provided the momentum for it to continue for several years after the Becks departed.

Criticisms of Rollo Beck

Many people who have worked with Beck's specimens have sung his praises, particularly the scientists who benefitted from his work. But Beck was not universally liked, and negative reviews sometimes came from other collectors who worked under him in the field. Beck had high expectations for himself and others, and pushed his workers as hard as he pushed himself. Inevitably after a few months of difficult conditions, workers would express some irritation with their expedition leader. Some of these concerns can be found in field journals of Beck's companions. Both Slevin (1931) and Quayle (WSSE, about 1921) complained bitterly that Beck would not give them sufficient time to document specimens (measurements, colors of soft parts, the ecology of the location). Beck's response, as they each relayed it, was basically, 'Collect! That's what you're being paid for!' Hunter, also on the 1905-06 expedition, saw a woodpecker finch fashion a tool from a twig, to dig grubs out of a limb. Hunter communicated this observation to Beck, and Hunter reports in his journal, "Beck reports having seen this same performance gone through with, two years ago. He is such a liar that I do not know whether to believe him or not." (Hunter field journal, January 4th, 1906, California Academy of Sciences Archives.) José Correia, originally from the Azores and very much admired as a collector by Robert Murphy, worked under Beck during the WSSE trip. Later, in a diary kept while collecting for AMNH on São Tomé and Príncipe, he told of his anger and frustration at Beck's treatment of him and his wife, Virginia. Correia sarcastically noted that one Christmas Beck presented him with 10-cent neckties, somewhat insulting and worse than useless presents in the Pacific islands. One lovely morning in Príncipe reminded him of the South Pacific "but these idea allways bring Beck to my mind and I hate him! I detest him forever so some times I hate south sea islands and they people but Beck's roten repution is the cause of these." (José Correia field notes, São Tomé and Príncipe, 15 March 1928, Library, American Museum of Natural History.) Indeed Beck's WSSE journals don't indicate that he was either patient or tolerant.

Even Beck's AMNH employers lost confidence in him toward the end, agreeing that he had been at sea and in command far too long, and that the best thing for both him and the expedition was to get him off the *France*. Pressure was applied, Beck finally wrote a letter of resignation and the Becks departed for Australia.

A career as long and productive as Rollo Beck's could not be without controversy either. Among these, Beck has been blamed for over-collecting birds and tortoises, for having collected without permits, and for introducing species to oceanic islands. Most prominent among these accusations is the possible extinction of two Galápagos tortoise subspecies.

The first species is the Fernandina tortoise, *Geochelone nigra phantastica*. Beck found it on 4 April 1906. He certainly had known that no tortoises had ever been collected from Fernandina, and he must have expected that it would be special. He finally encountered a single large male tortoise on the mountain top. He collected the specimen and spent a long moonlit night alone preparing it while fending off hundreds of ticks and eventually sleeping on the hard lava under an oil cloth. The next day, Beck carried the partially prepared carcass down the mountain most of the way himself. He summoned Joseph Hunter, who was off collecting cormorants along the coast, to help retrieve and finish preparing the tortoise specimen. The specimen was unusual — the shell was thin, it had

a distinctive "saddle-backed" shape, and it was the first specimen ever collected from Fernandina. They immediately suspected it was an undescribed species. (From the field journals of Beck, Hunter, Slevin, 3–7 April 1906.) Indeed it was undescribed and no other specimen had ever been collected before or since. Thus, Beck found and collected the only known member of its species, and the only evidence that a unique tortoise ever walked the lava-studded island of Fernandina.

There is greater hope for the second species as it still teeters on the brink of extinction. The Pinta tortoise, *Geochelone nigra abingdonii* has at least one remaining surviving individual. Notorious as "Lonesome George," he has no known female to mate with except from other *Geochelone nigra* subspecies, and his race appears doomed unless one can be found.

When the Webster-Harris Expedition traveled to Galápagos in 1897, it failed to find any Pinta tortoises for Rothschild. At Rothschild's beckoning, Rollo returned to Galápagos in 1901 to collect more tortoises, and this time Beck managed to find two Pinta specimens — one old large male that Beck skinned onshore, and a smaller individual that Beck collected alive (Nicholls 2006). Of course males, dead or alive, are no help to Lonesome George. Although it is not certain, the smaller tortoise was likely a female — it was smaller and had a simpler shell that was typical of females. Beck found this female trapped on an isolated beach, with several injuries due to a fall. Beck suspected that she would not make the trip to Tring, England, alive, and that Rothschild would prefer a scientific specimen to no specimen at all. He killed and skinned it and prepared the specimen. It is believed to be the only scientific specimen of any female in any museum collection (Nicholls 2006).

In September 1906, the California Academy's Galápagos Expedition collected four additional tortoises from Pinta, including three live male specimens; the fourth (CAS 8113) consisted only of a shell found relatively intact. Even in 1906, Slevin's field notes attested to the excellent tortoise habitat and that they found individuals almost immediately. This suggests that there were more tortoises on Pinta in 1906 when Beck and his team visited. Lonesome George is estimated to be between 60-80 years old. In recent years, another likely Pinta male was found in a Prague zoo. This individual was estimated to have hatched around 1960, so at least one pair must have lived until then. Researchers are now genetically testing all living Galápagos tortoises of unknown origin, looking for, among others, females that might have come from Pinta. Unfortunately none has been found so far; however, 39 half-Pinta half-other tortoises were repatriated to Pinta Island in May 2010, to resume their role as large herbivores in the ecology of the island.

The greatest destruction to the tortoises was wrought by whalers and fisherman who harvested tortoises by the hundreds for food, and later by goats introduced up until the mid-1900s that decimated their habitat (Van Denburgh 1914; Slevin 1959). Feral donkeys have trampled nests, and feral cats and dogs have depredated young. The Charles Island tortoise disappeared by the mid-1800s, presumably at the hands of hungry sailors. No laws were being written or enforced to protect the wildlife, so some feared that these species would disappear without any proper documentation. Beck had recorded the carnage in the killing pens himself with photographs from his early trips to the Galápagos, and these photos only inspired Rothschild and Loomis to fund trips to record the wildlife before it was gone. Even though Beck's specimens are among the last collected for scientific purposes, they were certainly not the last killed. Tortoise harvesting on the islands continued for decades afterwards.

The Guadalupe Caracara (*Caracara lutosa*) was a scavenging bird of prey and a relative of the falcons endemic to the small island of Guadalupe off Baja California, Mexico. Farmers on the island persecuted the caracara because they believed that they were killing goats. Ornithologists and collectors had a few in collections, and in the late 1890s, a fisherman arrived in San Diego with six of them for sale (Abbott 1933). Beck visited the island in December of 1900, and he encoun-

tered 11 individuals. He shot 9, but the other two got away. Based on their lack of fear and how many he saw in so short a time, Beck assumed they were common (Abbott 1933). But in 1906 when W.W. Brown and H.W. Marsden collected on Guadalupe, they found no trace of the caracaras despite tremendous effort (Thayer and Bangs 1908). Clinton Abbott (1933) assumed that Beck was probably the last person to see them alive.

During Beck's years leading the Whitney South Sea Expedition, numerous complaints were lodged with the American Museum, and rumors began to grow. In 1934, the Marquess of Tavistock, an aviculturalist interested in rare parrots, wrote a scathing letter to the *Auk* criticizing the American Museum and Beck for over-collecting endangered island birds (Tavistock 1934). Frank Chapman, Curator of Ornithology at the AMNH responded swiftly with actual collection records, arguing that the allegations were exaggerated and that the fears were unfounded (Chapman 1934). Eventually Chapman wrote a letter to *Science* (Chapman 1935) to squelch the rumors, but also to demonstrate the value of the ornithological work being done. The Whitney Expedition was among the first to document the avifauna of many of the islands, and already 44 publications had appeared based upon the collections. Chapman and others realized that these islands could reveal how birds evolve. He also realized that countless human practices were wiping out birds regardless of Beck's collecting, and that documenting the species and their ranges was key to understanding their status, even for conservation. Chapman was correct on every count. The Whitney collections remain the most complete record of Pacific Island birds ever made. They now represent the "baseline" for conservation work, and what we can compare with our present-day distributions. The number of publications stemming from those collections is astounding. The collections provided a fertile ground for the young Ernst Mayr who launched his lifelong work in evolutionary biology. Chapman effectively defended Beck, who appears to have operated under the necessary permits and within the ethical guidelines of the time.

New Uses for Old Collections

Precisely because these specimens were collected a century ago, they are extremely valuable to science. Each specimen carries a tag on which valuable data are written — the collector's name, field number, date, locality, and a variety of other information that cannot be gleaned from the specimen itself. Thus, the specimens themselves are the most tangible and complete record of those species from those times and places. The specimens become a source of information about the time and place as well as for descriptions of the species.

Researchers are now discovering a variety of new types of information that can be obtained from these old specimens. These include extracting DNA samples from feather or skin fragments, collecting pollen from the facial feathers of nectar feeders, analyzing stable isotope signatures from feather or bone fragments, or even surveying environmental contaminants or pollutants from feathers and eggshell.

The Galápagos finches are no exception. Workers have successfully extracted DNA from Beck's Galápagos birds for studies of the mockingbirds (Arbogast et al. 2006; Hoeck et al. 2009), Galápagos Hawk (Bollmer et al. 2006), and Darwin's finches (Tonnis et al. 2005). Patricia Parker from University of Missouri at St. Louis and her colleagues have demonstrated not only the ability to retrieve bird DNA from these 100-year old specimens, but they have also reliably recovered avian poxvirus DNA. This is allowing her research group to investigate the spread of diseases through finch populations and throughout the islands.

When these collections were made, some over 100 years ago, DNA was not yet discovered and genetics were largely unknown. No one could have anticipated these uses for their specimens. This

remains equally true today; we can only imagine what researchers 100 or 500 years from now might be capable of studying. For them, it will be important not only to preserve these old specimens that record the previous century, but also to create and preserve specimens from today's populations. If we continue to accumulate specimens from various time slices, future researchers may also be able to see evolution unfolding or document climate change and its impact on species.

Summary and Conclusions

Rollo Howard Beck spent some 65 years of his life collecting birds and contributing in various ways to ornithology, working from Alaska to Tierra de Fuego in North and South America, the Caribbean, and specializing in birds on Pacific Islands. The ornithological collections he built are among the largest contributions from any single collector. The large series and thorough collections have made possible the classic work by David Lack on Galápagos finches, and by Ernst Mayr on Southwest Pacific birds, just to name two of the most influential. He has been remembered in several obituaries and biographies, but mostly by the amazing series of beautifully prepared ornithological specimens in museums throughout the world.

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TABLE 1. Numbers of specimens in Ornithology collections that are attributed to R.H. Beck. An additional 842 herpetology specimens can be found in California Academy of Sciences and other institutions.

Museum Collection	**Specimens**
American Museum of Natural History*	36782
California Academy of Sciences	9526
Museum of Vertebrate Zoology, U.C.	4674
U. Michigan Museum of Zoology	923
Smithsonian	596
Museum of Comparative Zoology, Harvard	547
Other ORNIS	541
San Jose State University	354
Delaware Museum of Nat. History	261
Field Museum	165
Pacific Grove Museum of Natural History	118
Western Foundation of Vertebrate Zoology	44
Total	**54,351**

* Note that many museums are not yet fully digitized, so this number represents only Beck's specimens that have been duly documented and are easily searched. The AMNH is still entering their data from the Brewster-Sanford Collections and earlier, so these numbers represent a partial list of AMNH specimens collected after mid 1913. This is certainly an underestimate of the specimens worldwide that are attributed to Beck. AMNH accession cards suggest, however, that the full number for their collection may be as high as 44,204 (giving Beck a minimum number of documented specimens of around 62,000.) Some specimens are also attributed to multiple people (e.g., R.H. Beck and Assistants, R.H. Beck and E. Quayle, etc.) so we cannot say with certainty how many were skinned by Beck alone.

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Natural Selection, Speciation and Darwin's Finches

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Dedication

Bob Bowman's work on the functional morphology of beaks, and on the importance of learned song in the barrier to interbreeding, made a major contribution to current understanding of how Darwin's finches evolved. We pay tribute to him for these accomplishments, and gratefully acknowledge his invaluable advice that guided us in the early stages of our own research. Nobody knew the finches as well as Bob.

Speciation is a process of divergence of two lineages formed from one, culminating in the cessation of gene exchange. Darwin's finches in the Galápagos archipelago exemplify the three-step process envisioned by Charles Darwin: colonization of a new area; divergence in separate locations, chiefly through natural selection; and finally, the formation of a barrier to interbreeding between divergent lineages. In this chapter we summarize two major results from our long-term study of finches throughout the archipelago but principally on the small island of Daphne Major. First, we describe repeated evolutionary change in beak size and shape as a result of selection when the food environment changes owing to pronounced annual variation in rainfall. One factor contributing to selection is the presence of competitor species, as documented with an example of character displacement following the drought of 2003-2004. Second, we describe an example of Darwin's third step that we have recently observed. Colonization of Daphne Major Island by an immigrant *Geospiza fortis*, the medium ground finch, was followed first by interbreeding with resident *G. fortis* but then, after the residents experienced strong selection, intense inbreeding among members of the immigrant lineage and reproductive isolation from the residents. The key features that constitute the barrier to interbreeding are song and beak morphology. We draw attention to the importance of introgressive hybridization in the early stages of speciation and adaptive radiation in enhancing genetic variation and potentially facilitating further evolutionary change.

Times have changed (Fig. 1). Nonetheless we still grapple with the same problem of explaining the world's enormous biological diversity that Charles Darwin confronted 150 years ago (Darwin 1859). His answer in the *Origin of Species* is one long argument for how features of organisms can be explained as the product of adaptive evolution by natural selection and not by special creation. The absence of genetics made it inevitably incomplete. With a knowledge of genetics and a much better understanding of history, the search for explanations of fundamentals has continued. Seemingly impossible questions such as the origin of sex, multicellularity, and even life itself, are now within reach and are being addressed. But how are the numbers of species, the other side of the diversity coin, to be explained? The origin of new species, that is the production of two species from one, is the core process (Fig. 2). A population splits into two and the lineages diverge to a

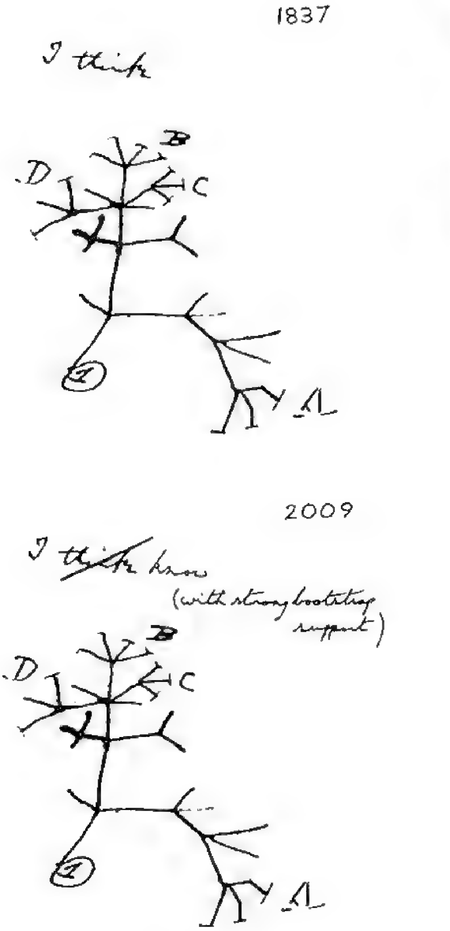

FIGURE 1. The first tentative thoughts of Darwin on phylogeny, reproduced from his Notebook B (above), contrasted with a confident modern rendering (below).

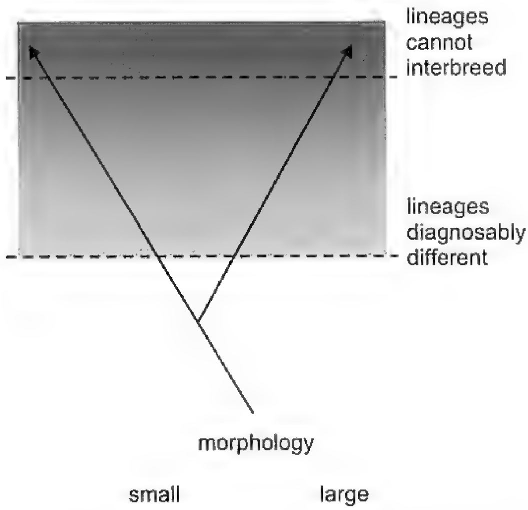

FIGURE 2. The evolution of two species from one. (From Grant and Grant 2008a).

point at which they are no longer capable of exchanging genes even if they attempt to do so. How does this happen? Darwin's thinking was much clearer on the circumstances than the causes, and clearer on how it began with divergence than how it finished with reproductive isolation. In his view geographical separation of populations was key to the beginning (Appendix 1). To one of his numerous correspondents he wrote "…those cases in which a species splits into two or three or more new species …I should think near perfect separation would greatly aid in their "specification" to coin a new word" (Letter to K. Semper, 1878; in F. Darwin 1887, vol. 3, p. 161). Fortunately that particular coin was dropped, and we use the term "speciation" instead.

To understand how the process is completed, we have to move forward almost a hundred years into the era of Mendelian genetics to find a clear, minimally sufficient, statement of the end-point of speciation from a population geneticist. Hermann Muller (1940) wrote "Thus a long period of non-mixing of two groups is inevitably attended by the origination of actual immiscibility, i.e. genetic isolation". Genetic drift would be enough, though natural selection would help (Coyne and Orr 2004).

The theme of this article is that many evolutionarily interesting events can occur between the two defining points of speciation, the start and the finish. This we have learned by following in Darwin's footsteps in the Galápagos, studying in detail the finches that were named after him by Lowe (1936) in recognition of their contribution to his theory of evolution by natural selection. While there is no single speciation process experienced by all organisms (Coyne and Orr 2004), individual studies such as the one we summarize can throw light on the tantalizing out-of-sight

processes that must have occurred in the past to give rise to diversity in the present; and, we hope, have some degree of generality.

Darwin's Finches

Darwin envisioned a three-step process in the formation of a new species: colonization of a new area; divergence in separate locations, when populations become adapted to novel environmental conditions through natural selection; and finally, the formation of a barrier to interbreeding between divergent lineages. He showed characteristic insight by suggesting that investigations of what we now call, "very young adaptive radiations" might provide windows through which we can view the processes involved. The finches named after him are ideal in many ways for doing this. They constitute a young adaptive radiation still present and fully intact in the environment in which they evolved over the last two to three million years. Thirteen biological species occur in the Galápagos archipelago and nowhere else, and a fourteenth occurs to the north on Cocos Island. On several of the islands, the natural vegetation is still intact with little or no influence of humans, so whatever we can discover about the relationship between finches and their environment can be directly extrapolated backwards in time without qualification to the conditions under which the finches evolved. Sadly one cannot say the same about other classical adaptive radiations elsewhere, such as the cichlid fish in the Great Lakes of Africa or the honeycreeper finches, *Drosophila* or Silversword Alliance of the Hawaiian archipelago.

Speciation

Figure 3 captures the geographical essence of the Darwinian conception of speciation: an allopatric phase with divergence and a sympatric phase with or without interaction. Evolutionary biologists have argued about the importance of various factors in these two phases (Coyne and Orr 2004; Price 2008). Genetic drift, for example, may or may not play an important role in divergence, but natural selection almost certainly does. Divergence in allopatry may be sufficient to allow coexistence in sympatry without any interaction (Stresemann 1936). David Lack (1945, 1947) argued this was un-likely, given the extreme similarity of some of the species, and that an interaction would probably occur in sympatry; competition for food, an ecological interaction, and limited interbreeding, a reproductive interaction. If the phenotypically most similar individuals of the two popu-

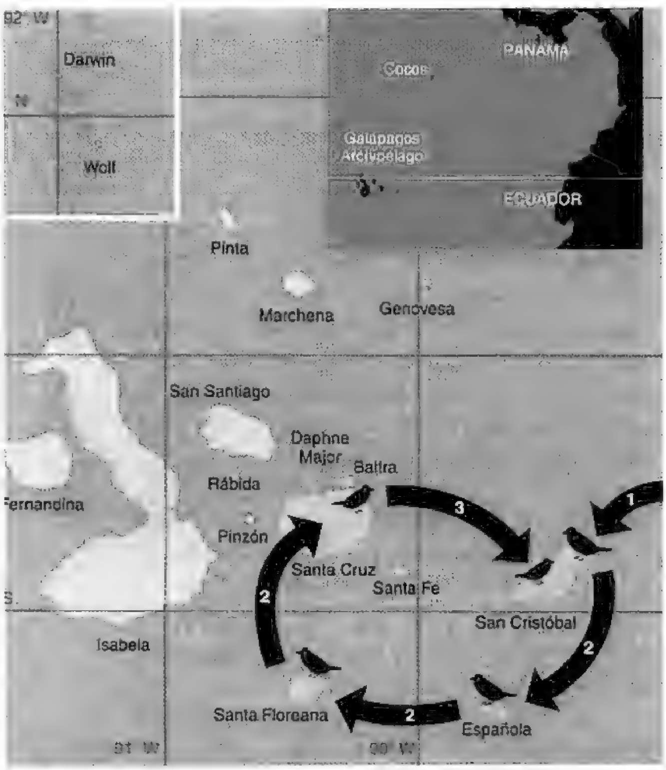

FIGURE 3. A representation of the three-step process of allopatric speciation. (From Grant and Grant 2002a). Note: San Santiago should be Santiago, and Santa Floreana should be Floreana.

lations suffered the most, because they were the most likely to compete for food and interbreed with a loss of fitness, then further divergence of the sympatric populations would be expected under natural selection, minimizing competition and the chances of interbreeding. The net result would be sustained coexistence of ecologically differentiated, reproductively isolated, species.

Adaptation in Allopatry

Populations of the same species differ morphologically and ecologically on different islands. For example, on Genovesa, the sharp-beaked ground finch (*Geospiza difficilis*) is small and has a small beak. Here the dry season food supply is dominated by small seeds, nectar, and pollen. On other islands, such as Pinta and Santiago, with larger and harder seeds, fruits, and arthropods, the beaks of *G. difficilis* are large and more robust. This is the kind of comparative association between organisms and their environment that is often used by evolutionary biologists to infer adaptive evolution by natural selection in the past (Bowman 1961).

The adaptive argument has been strengthened by a successful prediction of the beak sizes of finches on an island from a measure of their food supply (Schluter and Grant 1984). The distribution of seed sizes on an island gives a picture of the ecological opportunity available to the granivorous *Geospiza* species. It is sometimes referred to as an adaptive landscape. By randomly sampling the seed supply on 15 islands, we estimated 15 adaptive landscapes. The estimation procedure involved establishing a positive relationship between seed size and beak size, and between finch population biomass (or density) and seed biomass, across all species and all islands, and then integrating them. Each individual landscape has one or more peaks in expected population density in relation to beak size. We then compared the beak sizes of finches on each island with those beak sizes predicted from the expected density maxima (Fig. 4), and found four things. First, observed beak sizes of the four granivorous species of finches closely matched the predicted beak sizes. Second, no two species occupied the same position on the beak size axis in relation to a density peak. Third, no peak lacked a finch species. Fourth, the identity of the finch

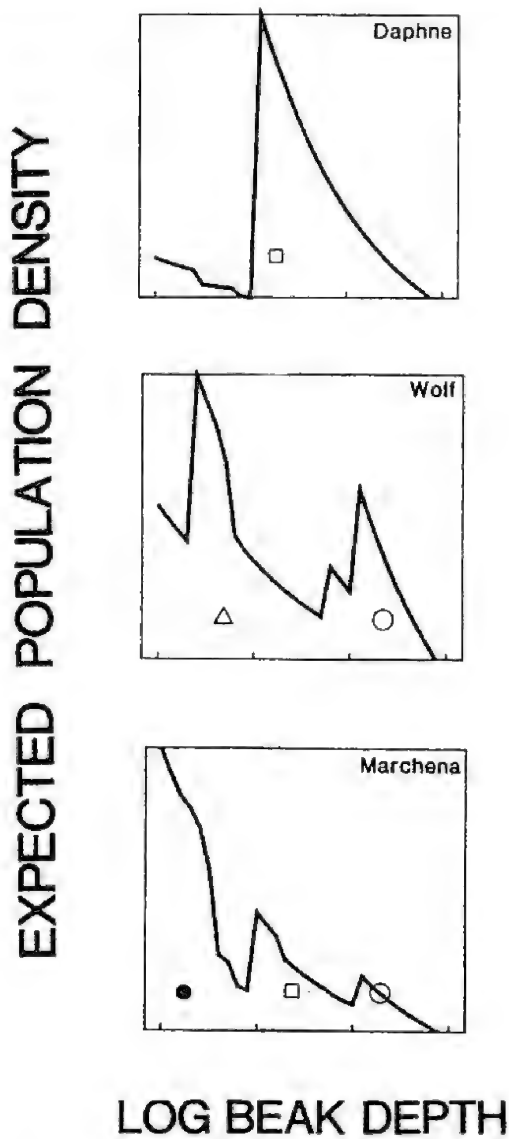

FIGURE 4. Alignment of *Geospiza* species with peaks in an adaptive landscape. Symbols: square *G. fortis*, triangle *G. difficilis*, open circle *G. magnirostris*, closed circle *G. fuliginosa*. (Adapted from Schluter and Grant 1984).

species beneath a peak sometimes changes from one island to another, but the alignment with the peak is maintained.

Adaptive modification of beak size involved changes in gene expression in development. Molecular genetic studies are beginning to unravel some of the complexities involved in the genetic control of ground finch beaks during development, and they are revealing differences between species in the timing and intensity of expression of signaling molecules. Expression of bone morphogenetic protein 4 (Bmp4) affects depth and width development (Abzhanov et al. 2004). At the same time, but independently, Calmodulin affects length development (Abzhanov et al. 2006). Just how these genes are regulated, differently in different species, is the subject of continuing research. Eventually it will be possible to identify how expression patterns differ among individuals of different beak size and shape within a single population. This information will be necessary in order to fully understand in genetic and ecological terms how phenotypic variation becomes transformed by natural selection, resulting in directional adaptive change and ultimately yielding a new species.

Natural Selection

Even though the adaptive argument is strongly supported by retrospective evidence, it would be improved if it could be documented by observations made while the process of adaptation is actually going on, i.e., observed forwards in time prospectively as opposed to being inferred backwards in time retrospectively (see Appendix 2). This we have been able to do on the small island of Daphne Major in the center of the archipelago.

Daphne is about 0.75 km in maximum length, 120 m high, and has never been settled by humans. We began a detailed study of the medium ground finch (*G. fortis*) and the cactus finch (*G. scandens*) in 1973. By capturing a large number of finches in mist-nets, then banding them uniquely, and measuring and weighing them before release, we were able to observe the feeding of finches of known measurements (Boag and Grant 1984). An early result from quantifying the feeding behavior of *G. fortis* was a clear demonstration that large-beaked members of the population were able to crack open large and hard seeds, whereas smaller members of the population were unsuccessful if they tried, or did not even attempt the task. As mentioned above, food size is a positive function of beak size; for mechanical reasons, the larger the beak the larger are the seeds and fruits that can be cracked open (Bowman 1961; Abbott et al. 1977; Herrel et al. 2005). We then determined that beak size was a highly heritable trait by regressing offspring measurements on their parent measurements. On a scale of 0 to 1 the heritability was approximately 0.75. This is unusually high, approximately comparable to the heritability of height in humans.

We had the good fortune to be present in 1977 when a severe drought affected the archipelago. It was not so fortunate for the finches, for 85 percent of the *G. fortis* population died (see last paragraph of Appendix 2). Survival was size-selective: large birds survived better than small ones (Fig. 5). The reason lay in their ability to crack or tear open the large woody fruits of *Tribulus cistoides* that were relatively common after the majority of small and soft seeds had been eaten.

As Darwin was aware from animal breeding, selection does not lead to a change in the next generation unless the trait under selection is inherited. Beak size and other morphological traits in Darwin's finches are heritable (Keller et al. 2001). Like their parents, offspring of the survivors of the drought that bred in 1978 were large, and distinctly larger than the population average before selection in 1976. Therefore evolution occurred in response to natural selection in 1977 (Fig. 5). In fact the average size of the offspring generation when measured at full adult size was remarkably well predicted by the breeder's equation, $r=h^2.s$ where r, the evolutionary response to selection is given by the product of the heritability of the trait (h^2) and a measure of the strength of selection (s).

This was not a solitary episode. Over the next 25 years we observed other episodes of selection, smaller in magnitude, associated with droughts (Fig. 6), oscillating in direction according to the particular food supply at the onset of the drought (Grant and Grant 2002b), and repeatedly resulting in evolutionary change in average beak size (Grant and Grant 2006).

Character Displacement in Sympatry

The foregoing example of natural selection involved no interaction between populations of finches, and therefore can be considered a model of how adaptive evolution occurs in allopatry, driven by a change in the environment. It would have been interesting to know if the population of *G. fortis* on the neighboring island of Santa Cruz had changed at the same time, but that was beyond our capacity to study. Almost 30 years after our first documentation of natural selection, we witnessed another selection episode in which interactions between species did occur (Grant and Grant 2006). This can be considered a model of how adaptive evolution occurs in sympatry, driven not only by a change in the environment but by competition for a limited supply of food.

A drought occurred in 2003 and 2004, and when it ended with rain falling in March of 2005, 90 percent of the *G. fortis* population had died. Almost the same amount of rain fell as in the 1977

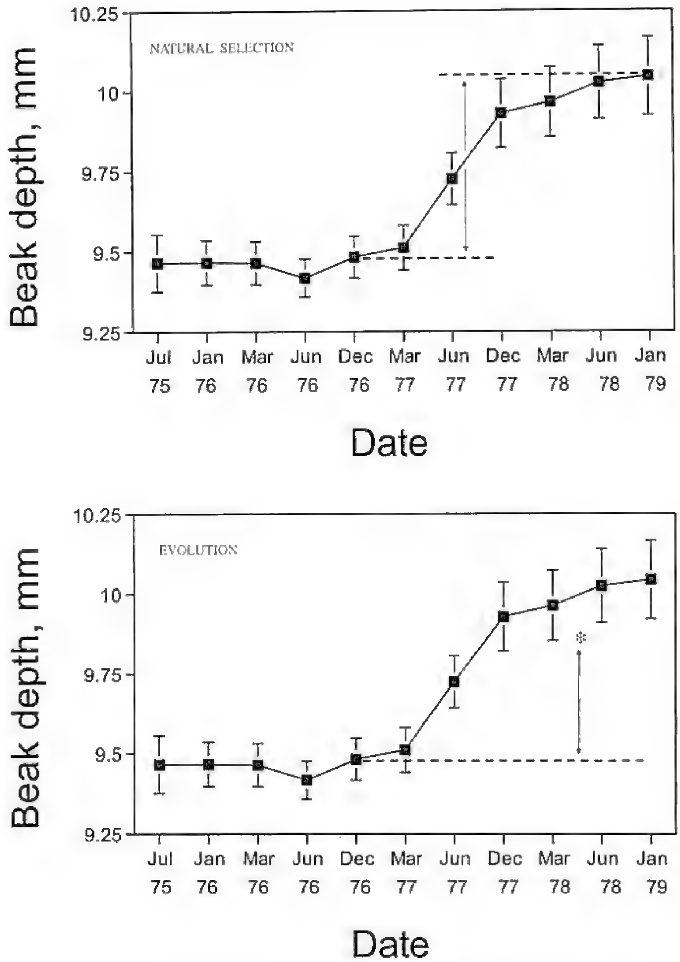

FIGURE 5. Natural selection in 1977 (above). The magnitude of the evolutionary response in the next generation (below) was determined by the strength of selection and the heritability of beak depth. (Modified from Grant and Grant 2008a).

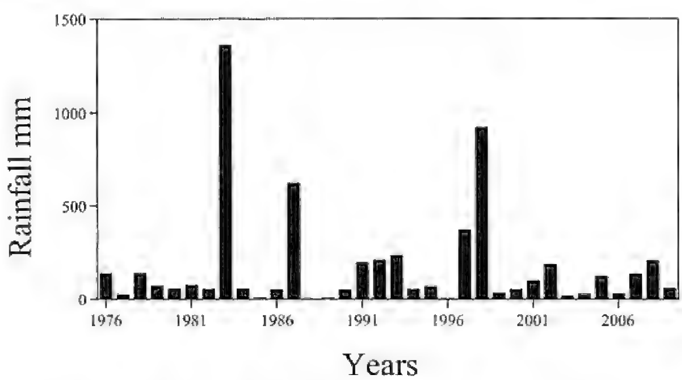

FIGURE 6. Annual variation in the rainfall on Daphne Major Island. (Modified from Grant and Grant 2008a).

drought, but this time birds with small beaks experienced a selective advantage (Fig. 7). The reason for this opposite response lay in another species, *G. magnirostris*, the large ground finch (Fig. 8). A breeding population of this species had become established on the island in 1983 at the beginning of an extraordinarily long and intense El Niño event that brought more than a meter of rain to the island. The population of *G. magnirostris* gradually increased in size, so that when the drought began in 2003, there were more than 300 alive on the island. Being superior competitors for *Tribulus* fruits, they had a strong effect on the survival of the larger members of the *G. fortis* population, and the average beak size of the *G. fortis* population fell to an unprecedented low value (Fig. 7). The offspring generation also had small beaks, as expected from the high heritability of beak size. Evolution by natural selection had occurred again, lead-

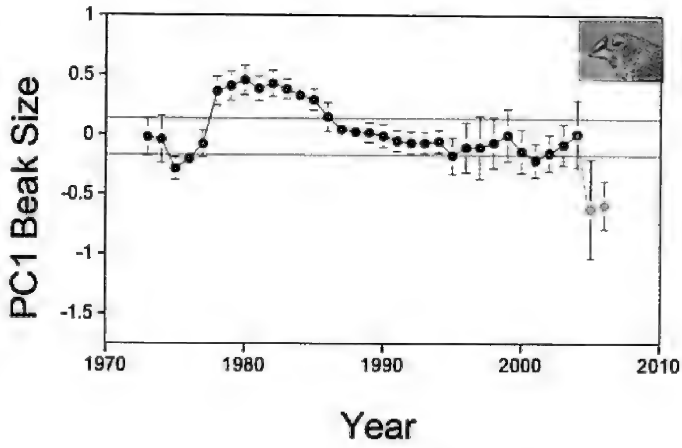

FIGURE 7. Natural selection on *G. fortis* in 2004-05 caused by competition with *G. magnirostris*. (From Grant and Grant 2006, 2008a).

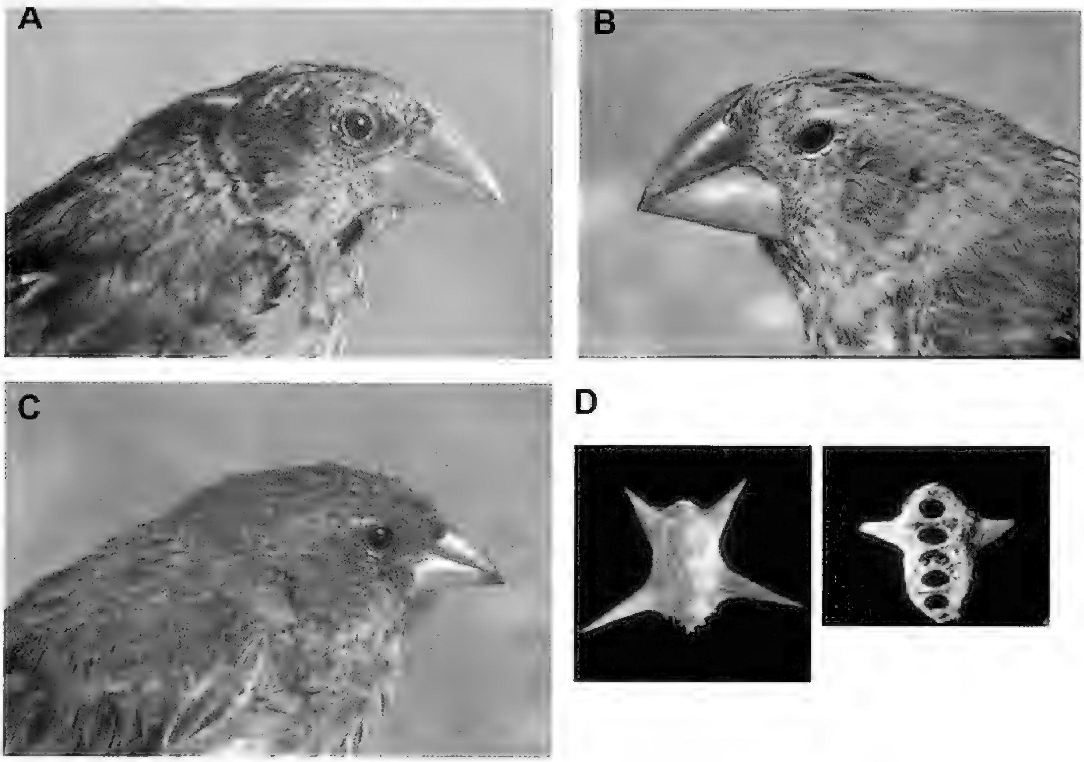

FIGURE 8. During a drought large *G. fortis* (A) compete with *G. magnirostris* (B) for the seeds of *Tribulus cistoides* (D) and die at a higher rate than the small *G. fortis* (C), which can only feed on small seeds. The result is natural selection (Fig. 7) and character displacement of *G. fortis*, an enhanced difference between the two species. (From Grant and Grant 2006).

ing to a divergence of the interacting populations. In other words, it was an example of character displacement (Grant and Grant 2006).

Reproductive Isolation

For sustained coexistence in sympatry, it is not enough that populations are ecologically different, they should be reproductively separate. How does reproductive isolation between coexisting species arise, and what constitutes the barrier to interbreeding? Darwin's (1871:192) answer was a combination of female preference for males with certain traits and divergence of the traits themselves. The first question for Darwin's finches is therefore what are the male traits?

Many species of birds differ in plumage pattern and/or courtship behavior. Not so the Darwin's finches. Instead they differ in song and morphology, especially beak size and shape. The role of these two factors in species discrimination and mate choice has been tested experimentally. A series of experiments on several islands with pairs of stuffed museum specimens showed that ground finches discriminate between their own and another species on the basis of visual cues in the absence of song and movement (Ratcliffe and Grant 1983). Another set of experiments with playback of tape-recorded song similarly demonstrated discrimination on the basis of acoustic cues alone, in the absence of any visual cues (Ratcliffe and Grant 1985). These two sets of cues function together, and research by Robert Bowman (1983) with captive finches gives clues as to how this happens. Using sound-proof chambers, he demonstrated that song is learned early in life in an imprinting-like process. The sensitive period of the offspring appears to be short, from approximately day 10 to day 40 of age, when they are dependent on their parents for food. The offspring are in frequent visual contact with both parents at this time. Thus paternal song and the appearance of both parents are learned early in life, and they are used later when mates are chosen (Grant and Grant 1998). The learning process, sexual imprinting, usually constrains the choice of mates to a member of the same species, but not always.

The second question for Darwin's finches is how do the two male traits, beak morphology and song, diverge? Beaks diverge as a result of different selection pressures on different islands, because the islands have different food supplies and different constellations of species competing for it (Abbott et al. 1977; Smith et al. 1978; Schluter and Grant 1984). Divergence in song features is less well understood and deserves study. Songs may diverge as a result of non-genetic adjustments to island-specific habitat features, or their divergence may be independent of environmental conditions and instead they may be attributed to chance factors operating in the establishment of a new population (Grant and Grant 2008a).

A Barrier that Leaks

Species-specific song and morphology can be thought of as two elements that jointly constitute a pre-mating barrier to interbreeding. Very occasionally the barrier leaks; species interbreed. Although it is rare this is important as it allows us to determine if a post-mating barrier between species also exists. Hybridization occurs when the imprinting process is perturbed, for example by the death of the father while the offspring are in the nest. If another species nests nearby, the offspring may learn the song of that species. We have also known of a *G. fortis* nest being taken over by a pair of *G. scandens*, resulting in a fortis egg being raised by the *G. scandens* pair. In this case the cross-fostered male *G. fortis* sang a *G. scandens* song. *G. fortis* and *G. scandens* hybrids show the same imprinting as the two parental species, and choose mates according to the song sung by their fathers.

In the first ten years of the study hybrids did not survive long enough to breed, and we thought they might have suffered from intrinsic weakness. However, an alternative possibility was a lack of seeds in the dry season suitable for birds of their intermediate size, because this was a time when *Tribulus* fruits dominated the composition of the dry season food supply. This latter possibility turned out to be correct because from 1983 onwards hybrids have bred. The 1983, 1987 and 1991 cohorts of hybrids (and backcrosses) have survived as well as if not slightly better than the parental species that gave rise to them (Fig. 9). They attracted mates, laid eggs and fledged offspring with as much success as the parental species (Grant and Grant 1992). Thus they are not at any apparent fitness disadvantage, in terms of either viability or fertility. These species are reproductively isolated from each other by a pre-mating barrier that leaks, rarely, and not by a post-mating barrier. There is no intrinsic post-zygotic isolation.

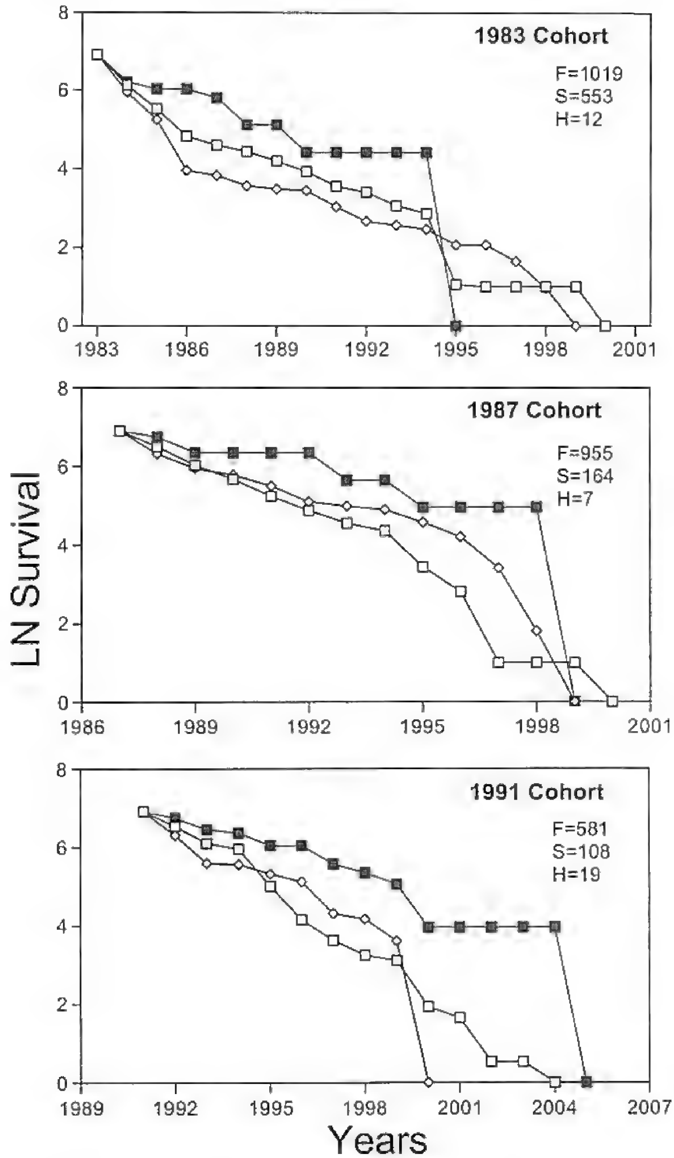

FIGURE 9. Survival of hybrids (including backcrosses) (H) in relation to the two parental species, *G. fortis* (F) and *G. scandens* (S). Symbols: Diamonds *G. fortis*, open squares *G. scandens*, filled squares hybrids. (From Grant and Grant 2008a).

Speciation in Reverse

The net effect of gene exchange between two genetically compatible species is morphological convergence, reversing the process of divergence that gave rise to the two species in the first place. This is what *G. fortis* and *G. scandens* are experiencing now on Daphne (Fig. 10). If gene exchange and convergence continue unchecked, they will eventually lead to the fusion of the species into a single panmictic population. In this case speciation will have collapsed. However, convergence may be arrested by a change in environmental conditions. Fission will once again occur if the environment reverts to a state similar to that in the 1970s when hybrids did not survive long enough to breed. We consider it likely that over the long course of finch history there have been numerous oscillations in cli-

matic and botanical conditions, causing finch populations to alternate between fission and fusion (Grant and Grant 2008b). Eventually fission becomes permanent. How does that happen?

Again, the Daphne study provides valuable insight. The barrier to interbreeding becomes watertight, and interbreeding ceases altogether, when morphological differences are pronounced. On Daphne *G. magnirostris* has not hybridized with the two resident and distinctly smaller species *G. fortis* (Fig. 8) and *G. scandens*, despite some occasional misimprinting. At least nine male *G.. fortis* have misimprinted on *G. magnirostris* song over a period of 25 years. If song was the only cue used in the choice of a mate *G. fortis* should have bred with *G. magnirostris*, as they have done with *G. scandens*. This has never happened. Instead, misimprinted *G. fortis* that have nested near a pair of *G. magnirostris* have been repeatedly harassed by the male. In fact the only misimprinted *G. fortis* male to have successfully bred practically gave up singing, and then obtained a conspecific mate. In this case a mate was chosen on the basis of morphology and song apparently played no role. Consistent with the relative importance of the morphological difference between species, *G. fortis* do occasionally pair and apparently breed with *G. magnirostris* on Santa Cruz where they are larger than on Daphne and the difference between the species is smaller. The likelihood of hybridizing diminishes with increasing divergence, and it diminishes with time if divergence is time-dependent.

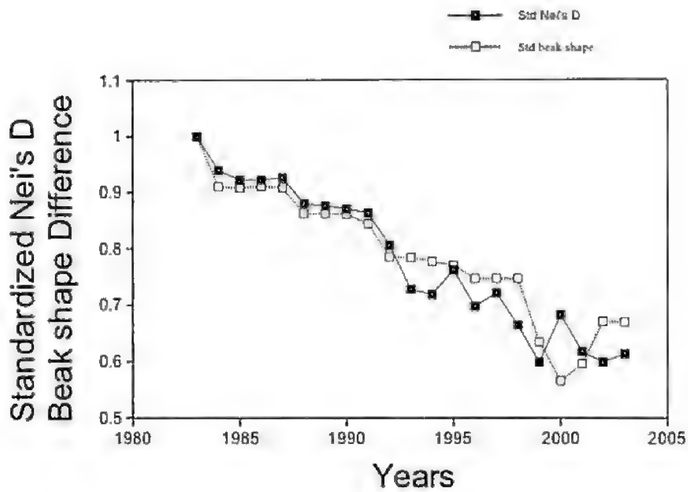

FIGURE 10. Convergence of *G. fortis* and *G. scandens* in microsatellite profiles (closed symbols) and beak shape (open symbols) as a result of introgressive hybridization. (From Grant and Grant 2008a).

Evolutionary Potential of Hybridization

Introgressive hybridization, once thought to be rare and mainly a phenomenon of plants, is now known to occur in a variety of taxa, from micro-organisms to macro-organisms (Schwenk et al. 2008). We have speculated that it does more than cause a collapse of two species. Under favorable ecological conditions it might allow one or both of the hybridizing species to evolve faster, or along a new trajectory, (Grant and Grant 2008b). This follows from the increase in additive genetic variance underlying continuously varying, ecologically meaningful, traits like beak size, and from non-additive effects of combining different sets of genes. Introgression also weakens the genetic correlation between traits when the hybridizing species differ in their allometries. The enhanced genetic variation and altered genetic covariation relaxes genetic constraints on further evolution. For populations in the early stages of speciation introgressive hybridization could be an important factor contributing to change that culminates in the cessation of interbreeding.

Establishment of Reproductive Isolation

Perhaps the most remarkable discovery on Daphne in recent years has been observations that show how a new lineage becomes reproductively isolated from a relative. They also illustrate one

potent way in which hybridization can contribute to speciation.

Instead of beginning with a small group of immigrants, as happened with *G. magnirostris* in 1983 (Gibbs and Grant 1987, Grant and Grant 1995), it began with a single immature male that arrived in 1981 (Grant and Grant 2009a). This was an exceptionally large *G. fortis* individual, carrying *G. scandens* genes, and it probably arrived from the adjacent large island of Santa Cruz. It first bred, in 1983, with a *G. fortis*, also carrying *G. scandens* genes, and again in 1987 with another *G. fortis*, also carrying *G. scandens* genes. Thus from the outset the lineage was a homoploid hybrid lineage. We followed the fate of the lineage from generation 0 (the immigrant) to generation 6. At generation 4, a brother-sister mating occurred at a time (2005) when no other member of the lineage had survived the drought of 2003–05. From then on the lineage was entirely endogamous: it had become reproductively isolated from the rest of the *G. fortis* population on the island. This rare example of reproductive isolation observed to arise following immigration reveals how chance may play a large role in creating a barrier to gene exchange in small populations: in colonization and establishment, in the initial mating, and in the switch from outbreeding to inbreeding.

Whether the barrier is transitory or enduring, the example provides insight into how reproductive isolation has arisen in the past during the radiation. Isolation depended on divergence in an ecologically significant trait, beak size, in allopatry (Fig. 3). As discussed above, the same trait signals species identity in a courtship context (Ratcliffe and Grant 1985). Thus the observations are consistent with ecological theories of speciation in which a barrier to interbreeding arises as a byproduct of divergence in allopatry (Dobzhansky 1937; Schluter 1996). However, beak size is not the only component of the barrier, the other important one is song. The song of the immigrant and his descendants appears to be unlike any other either heard by us or tape-recorded on Santa Cruz or other islands, but is similar to one of the songs sung by *G. fortis* on Daphne. Therefore, we believe that the immigrant was influenced by local song on Daphne when learning to sing its own song for the first time in 1983, but it did not copy local song accurately, and thus, as a result, began a new song tradition on the island.

Should the immigrant lineage be considered a new species? Darwin might have replied "yes", for in Notebook II (p.161) he wrote "My definition of species has nothing to do with hybridity [hybrid sterility], is simply, an instinctive impulse to keep separate, which no doubt be overcome, but until it is these animals are distinct species." (Kottler 1978). Our response to the same question is "too early to tell". Divergence might collapse with interbreeding (e.g., see fig. 10) because the impulse to keep separate is learned and not instinctive and therefore perturbable. Recognizing that possibility, and with modern knowledge of hybridization, Darwin would have drawn his famous "I think" phylogeny differently (Fig. 11) to illustrate reticulation.

Summary

Speciation is a process of divergence of two lineages formed from one, culminating in the cessation of gene exchange. Darwin's finches in the Galápagos archipelago exemplify the three-step process envisioned by Charles Darwin: colonization of a new area; divergence in separate locations, chiefly through natural selection; and finally, the formation of a barrier to interbreeding between divergent lineages.

In this paper we summarize the findings from a long-term study of the finches designed to throw light on this important part of evolutionary biology. Finch species differ principally in beak size and shape. Evolution of beak size by natural selection has been inferred from indirect evidence, including a successful prediction of beak sizes on several islands according to island-specific distributions of seed sizes. On Daphne Major Island the evidence is direct: the medium ground

finch population (*G. fortis*) has been subject several times to natural selection during droughts, most notably in 1977. This is a model of divergent evolution in allopatry. Daphne was colonized by the large ground finch (*G. magnirostris*) in 1983, and many years later *G. fortis* diverged from it during a severe drought, becoming smaller on average as a result of a competitive interaction and natural selection. This example of character displacement is a model of divergent evolution at the secondary sympatric phase of speciation.

The barrier to interbreeding develops in allopatry as a result of divergence in beak morphology and song. Paternal song and the appearance of both parents are learned early in life, and they are used later when mates are chosen. The process is sexual imprinting, and the result is pre-mating reproductive isolation from coexisting species that differ in song and morphology. One such case is described, in which an immigrant lineage of *G. fortis* became reproductively isolated from resident *G. fortis* within two-four generations. The barrier to interbreeding occasionally leaks, hybridization ensues, and the hybrids backcross to one species or the other depending on the song of their fathers. The immigrant lineage was started with the immigrant, a backcross from *G. scandens* to *G. fortis*, breeding with a resident of similar genetic constitution. There is no intrinsic post-zygotic isolation among the ground finch species that results from genetic incompatibilities. When feeding conditions suitable for hybrid survival persist for many years, species converge through introgression. Speciation then goes into reverse. We consider it likely that over the long course of finch history there have been numerous oscillations in climatic and feeding conditions, causing finch populations to alternate between fission and fusion. Eventually, the species diverge so much they no longer interbreed; gene exchange ceases and fission becomes permanent.

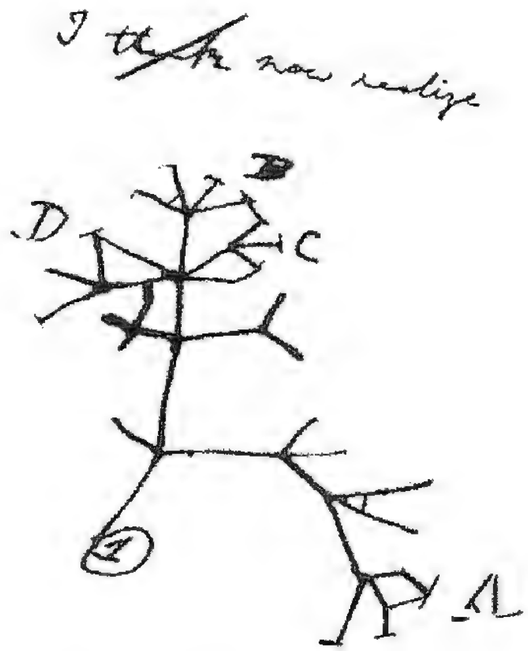

FIGURE 11. How Darwin might have depicted his thoughts on phylogeny, with allowance for reticulation caused by introgressive hybridization.

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Appendix 1

Darwin and the Absence of Sympatric Speciation

We have placed our discussion of speciation in the framework of allopatric speciation because an archipelago with many discrete islands is the ideal allopatric context. Sympatric speciation is a possible alternative to allopatric speciation. It has been offered as an explanation for the exceptional, bimodal, pattern of variation in the beaks of *Geospiza fortis* on the large island of Santa Cruz (Ford et al. 1973; Huber et al. 2007; Hendry et al. 2009). Other explanations for the bimodality, involving immigration from a differentiated population on another island, or introgressive hybridization, could explain the bimodal pattern within the allopatric speciation framework (Grant and Grant 2009b). Distinguishing between allopatric and sympatric origins of divergence is difficult if not impossible. The important features of sympatric speciation — assortative mating and disruptive selection — are not distinguishable from assortative mating and diversifying selection at the secondary contact phase of allopatric speciation (Grant and Grant 2009b). Such modern debates (Coyne and Orr 2004) have their roots in Darwin's attempts to understand the origin of species.

In his notebooks on transmutation Darwin developed a theory of species as reproductively isolated populations that had evolved "cross-sterility and aversion to intercrossing" in geographical isolation (Kottler 1978). In later writings, for reasons explored by Ghiselin (1969) and (Kottler (1978), he transferred his emphasis to the gradual process of evolutionary change in speciation and the difficulties encountered in identifying a line of demarcation between varieties and species. By doing so, and without stressing reproductive isolation that evolved in geographical isolation, he made himself vulnerable to the criticism of replacing a theory of allopatric speciation with one of sympatric speciation (Mayr 1992); a failed theory in the view of Mayr (1994). Ambiguities in Darwin's writing, inconsistencies (Thompson 2009), omissions, and, confusingly, two different meanings for the word variety (Mayr 1992), all contributed to the idea that Darwin argued for speciation occurring entirely sympatrically (Kohn 2008). We draw the opposite conclusion from reading the *Origin* (ch. 3) and his big book on Natural Selection (ch. 6). Divergence in allopatry ("different districts") is frequently stressed explicitly, and when it isn't the writing is non-specific with regard to geography, that is to say geography-neutral. Asexual plants are a possible exception (Stauffer 1975:241). Extinction and replacement of one form by another (e.g., Stauffer 1975:227, 242), and the filling of different ecological niches, are not exceptions (e.g., Stauffer 1975:234, 238; see also Mallett 2008), even though they have been considered as such (Mayr 1992).

The exact role of geographical isolation in speciation was the subject of correspondence between Moritz Wagner and Charles Darwin. In a letter to Wagner in 1868 Darwin wrote: "But I must still believe that in many large areas all the individuals of the same species have been slowly modified, in the same manner, for instance, as the English race-horses have been improved, that is by continued selection of the fleetest individuals, without any separation. But I admit that by this process two or more new species could hardly be found within the same limited area; some degree of separation, if not indispensable, would be highly advantageous" (Darwin 1887, vol. 3, p. 158).

Anagenetic (phyletic) evolution without speciation was implicitly contrasted in this passage with speciation through cladogenesis, albeit somewhat fuzzily on the role of isolation ("if not indispensible"). Eight years later Darwin sharpened the distinction between these two modes of evolution in a letter to Wagner in attempting to eliminate any ambiguity:

> I think you have misunderstood my views on isolation. I believe that all the individuals of a species can be slowly modified within the same district, in nearly the same manner as man effects by what I have called the process of unconscious selection . . . . I do not

> believe that one species will give birth to two or more new species as long as they are mingled together within the same district. Nevertheless I cannot doubt that many new species have been simultaneously developed within the same large continental area; and in my 'Origin of Species' I endeavored to explain how two new species might be developed, although they met and intermingled on the borders of their range. It would have been a strange fact if I had overlooked the importance of isolation, seeing that it was such cases as that of the Galapagos Archipelago, which chiefly led me to the study of the origin of species (Darwin 1887, vol. 3, p.159).

Darwin is arguing against sympatric speciation with the sentence "…I do not believe that one species will give birth to two or more new species…within the same district", and has added the phrase "…mingled together within the same district" to emphasize lack of spatial separation, i.e., syntopic and sympatric in modern terms.

The modern theory of ecological speciation (Schluter 1996, 2009) avoids most of these interpretational difficulties by emphasizing ecology rather than geography. Identifying the geographical origin of species remains a challenge.

Appendix 2

Darwin and the Absence of Case Studies of Speciation

A question we have often asked is why did Darwin not attempt to explain individual cases of speciation, even in outline, instead relying on general, non-specific, arguments? One possible answer, from a modern perspective, is that he lacked an estimate of phylogenies to identify ancestral and derived species. We think this is unconvincing. In England one does not need a phylogeny to know, for example, that willow warblers, wood warblers and chiff-chaffs are very similar in appearance (e.g., see White 1877) and therefore probably closely related. Given Darwin's speculative mind and his knowledge of phylogenies as conceptual (Fig. 1) and empirical devices (Darwin 1859, Fig. 1) he could have constructed one easily to make a point about descent with modification. In fact Darwin discussed these particular species in his unpublished *Natural Selection* manuscript (Kottler 1978; Stauffer 1975).

A more convincing answer is to be found in the Introduction to the *Descent of Man and Selection in Relation to Sex*; individual cases, real or contrived for illustration, could be dismissed whereas repeated and hence general patterns could not.

> …I have been led to put together my notes, so as to see how far the general conclusions arrived at in my former works were applicable to man. This seemed all the more desirable as I had never deliberately applied these views to a species taken singly. When we confine our attention to any one form, we are deprived of the weighty arguments derived from the nature of the affinities which connect together whole groups of organisms—their geographical distribution in past and present times, and their geological succession. (Darwin 1871, p.2).

This attitude, and his belief that natural selection was infinitesimally slow, explains why he was not alert to the possibility of natural selection occurring near home. As a result he may have missed important evidence for his principle. During the severe winter of 1854–55 as many as four fifths of the birds in southern England perished (Darwin 1859:68). Selection may have been at work in his own garden and woods, for mortality was similar to what we observed among the medium ground finches in 1977.

Close of Darwin Symposium Presentations

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